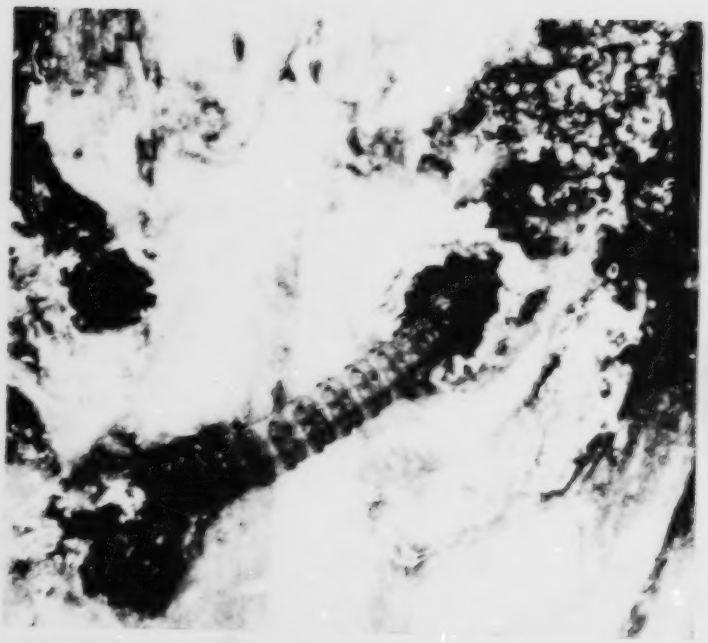

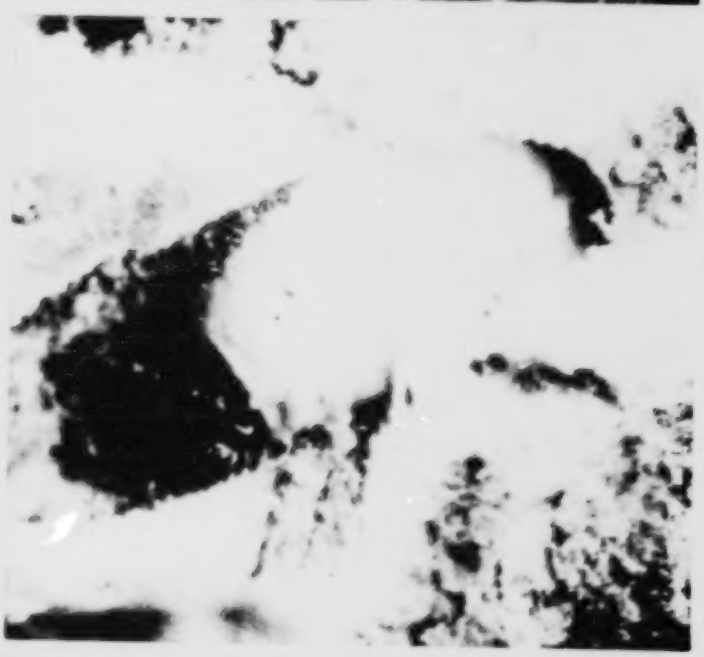

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Cover Photos: Clockwise from top left: Spruce coneworm, *Dioryctria reniculelloides* Mut. and Mun.; fir coneworm, *Dioryctria abietivorella* (Grt.); red squirrel, *Tamiasciurus hudsonicus* (Erxleben); spruce cone beetle, *Ernobius bicolor* White.

PROCEEDINGS - CONE AND SEED PEST WORKSHOP,
4 October 1989
ST. JOHN'S, NEWFOUNDLAND, CANADA

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FOREWORD

This report documents the proceedings from the cone and seed pest workshop held in St. John's, Newfoundland on 4 October 1989 in association with the annual meeting of the Entomological Society of Canada. The presentations by researchers from Forestry Canada, Lakehead University and the United States Department of Agriculture Forest Service covered a wide range of topics. Some papers reviewed key insect and disease pests, while others addressed insect control by semiochemicals, problems in sampling and damage assessment, clonal variation and damage susceptibility, seed orchard design to minimize losses to pests, and squirrel damage and management.

I thank the authors and reviewers of the proceedings for their contributions and cooperation. I am also grateful to Mary Gillingham, Joan Rockwood, Hildegarde Dunphy and Doug Rex of Forestry Canada (Newfoundland and Labrador Region) for preparing the manuscript for publication and to Michel Savard (Secretary of State, St. John's) for translating the abstracts. Funding for publication was generously provided by Forestry Canada (HQ).

Richard J. West
St. John's, Newfoundland
Canada

April 1990

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RESEARCH ON CONE AND SEED INSECTS IN NORTH AMERICA
PAST, PRESENT AND FUTURE

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ABSTRACT

Entomologists first described insects attacking cones and seeds of North America conifers more than 100 years ago. Pest status for these insects coincided with large investments in applied tree improvement programs, particularly for Douglas-fir in the Pacific Northwest and southern pines in the Southeastern United States. Early research dealt with insect identification and biology; later studies determined the relative importance and impact of these pests. Research clearly showed that prevention of insect attacks is essential for reliable production of genetically improved seeds in managed seed orchards. With few exceptions, control is by chemical insecticides. Current research is aimed at clarifying the taxonomy of major pest species, studying details of insect biologies, finding alternatives to chemical sprays, and developing methods to predict the need for and better time control procedures. Future research will continue to focus on cone and seed insect pests of the major conifer species until alternate methods of propagation, such as rooted cuttings or tissue culture, become commercially practical and displace seed production.

RÉSUMÉ

Les entomologistes ont commencé à décrire les insectes ravageurs des cônes et des graines de conifères en Amérique du Nord il y a plus d'un siècle. L'investissement de sommes considérables dans la recherche appliquées sur l'amélioration génétique des arbres, notamment dans le cas du Douglas taxifolié sur la côte nord-ouest du pacifique et du pin dans le sud-ouest des États-Unis, a coincidé avec la désignation de ces insectes comme ravageurs. Les premières recherches ont porté sur l'identification et la biologie des insectes: les études subséquentes ont détermine l'importance relative et l'impact de ces espèces. Ces recherches ont clairement indiqué la nécessité de prévenir les dégâts dus aux insectes dans les vergers à graines pour obtenir régulièrement des semences génétiquement supérieures. A quelques exceptions près, cette prévention se fait au moyen d'insecticides chimiques. Actuellement, les recherches visent à clarifier la taxonomie des principales espèces de ravageurs, à étudier leur biologie de façon détaillée, à trouver des solutions de rechange aux arrosages chimiques, ainsi qu'à élaborer des méthodes détaillées pour prédire l'opportunite des interventions et la période optimale des traitements. Les recherches sur les ravageurs des cônes et des graines des principales essences deconifères se poursuivront, et ce, jusqu'à ce que de nouvelles méthodes de propagation, comme les boutures racinées ou la culture des tissus, trouvent une application commerciale qui leur permette de supplanter la production des graines.

INTRODUCTION

Cone and seed insects were of interest to early entomologists long before modern forestry was practiced in North America. Thomas Say described the leaffooted pine seed bug, Leptoglossus corculus (Say) in 1831 (Say 1831), but 135 years passed before it became a "pest" (DeBarr 1967). With the advent of forestry in North America during the early 1900's, problems of poor natural regeneration of forest trees were first attributed to cone and seed insects. Harrington (1902) reported that "the ground beneath the trees was strewn with aborted and undeveloped cones..." killed by the white pine cone beetle, Conophthorus coniperda (Schwarz). However, pest status for most of these insects coincided with large financial investments in applied tree improvement programs (Zobel and Talbert 1984) during the 1950s, particularly for Douglas-fir, Pseudotsuga menziesii (Mirb.) Franco, in the Pacific Northwest and southern pines, Pinus spp., in the Southeastern United States.

Research Constraints - Forest entomologists working on cone and seed insects face a number of difficulties. A major problem is that they often must work in the tops of tall trees. Also, pest insect complexes differ by host and, compared to many forest insects, relatively low populations cause significant losses. Most species spend a major part of their life cycles hidden within cones or seeds, beneath bark or in the duff or soil. In addition, many are nocturnal or undergo periods of extended diapause. Often, damage detection is difficult, with similar damage symptons caused by different species. In spite of these constraints, a small cadre of researchers, often with few funds and limited technical support, have made significant progress.

Progress Through Cooperation - Forest entomologists working on cone and seed insects have always been a close group, excited about their research and willing to exchange information and collaborate on studies. To prevent duplication in the rapidly growing field of cone and seed insect research, early pioneers in the field, including Alan Hedlin, Norman E. Johnson, and Edward P. Merkel shared ideas, plans, successes, and failures by informal newsletter. N.E. Johnson served as the first editor of the Cone and Seed Insect Newsletter, which circulated semiannually from 1960 until 1983. It was then assimilated by the International Union of Forestry Research Organizations (IUFRO) Working Party S2.07-01 Cone and Seed Insect Newsletter, which is now sent to 210 scientists in 39 countries. Our IUFRO Working Party has met twice in North America: first in Athens, Georgia, USA, under sponsorship of the USDA Forest Service (Yates 1984) and last year in Victoria, British Columbia, Canada, hosted by Forestry Canada (Miller 1989). Dr. Alain Roques (France) and I are the current Working Party Co-chairmen.

Since the 1950's cone and seed insect research has been conducted by scientists at forestry research laboratories and

universities throughout the continent. However, research has been continuous at the Forestry Canada Pacific Forestry Centre in Victoria, British Columbia, and at the USDA Forest Service Southeastern Forest Experiment Station, Athens, Georgia, and Olustee, Florida.

By 1969 more than 700 papers had been published on cone and seed insects of North America (Barcia and Merkel 1972). During the past 20 years that number has more than doubled. I have tried here to cite papers that have obvious merit or made a unique research contribution. Examples are from throughout North America, but space does not permit me to cite many papers with valuable contributions to our knowledge of cone and seed insects.

CONE AND SEED INSECT BIOLOGY

Bionomics - North American cone and seed insects have both similarities and differences among the various life-zones (Merriam 1898), largely dictated by climate, geology, soils, and available host trees. Beginning in the late 1950's numerous reports were published on species composition, symptoms of damage, and general importance or frequency of occurrence of insects attacking seeds and cones of various conifers: red pine, P. resinosa Ait., (Lyons 1956); slash and longleaf pines, P. elliottii Englem. var. elliottii and P. palustris Mill., (Ebel 1963); douglas-fir, Pseudotsuga menziesii (Johnson 1963a, Hedlin and Johnson 1963); grand fir, Abies grandis (Dougl.) Lindl., (Hedlin 1967a); western white pine, P. monticola Dougl., (Schenk and Goyer 1967); shortleaf pine, P. echinata Mill., (Franklin and Coulson 1968); ponderosa pine, P. ponderosa Laws., (Kinzer 1972); and loblolly pine, P. taeda L., (Yates and Ebel 1978). Much of this early research reported in journals and technical publications has been summarized in regional guides (Keen 1958, Hard 1964, Hedlin 1974, Ebel et al. 1976, Ruth et al. 1982), in annotated bibliographies (deGroote 1986a, 1986b), and in a comprehensive guide to cone and seed insects of North America (Hedlin et al. 1980). Similar studies continue to be made in previously unexamined locations, such as Mexico (Cibrian-Tovar et al. 1986) or on tree species of limited commercial importance, such as white fir, Abies concolor (Gord. and Glend.) Lindl. (Shea 1989). Little research has been done on insects that destroy the seeds of hardwood trees (Barber and DeBarr, unpublished), primarily because conifers dominate commercial forestry in North America.

Early research studies dealt with biologies of important cone and seed insects. Excellent examples include: the balsam-fir seed chalcid, Megastigmus specularis Walley, the Douglas-fir cone moth, Barbara colfaxiana (Kearfoot), the Douglas-fir cone gall midge, Contarinia oregonensis Foote and the ponderosa pine seedworm, Cydia piperana (Kearfott) (Hedlin 1956, 1960, 1961, 1967b); the white pine cone beetle, C. coniperda (Godwin and Odell 1965); the slash pine seedworm, Cydia anaranjada Miller (Merkel 1967a); the southern pine coneworm, Dioryctria amatella Hulst. (Coulson and

Franklin 1970); the ponderosa pine cone beetle, Conophthorus ponderosae Hopkins (Kinzer et al. 1970; and the shieldbacked pine seed bug, Tetyra bipunctata (Herrich-Schaffer) (Cameron 1981).

Taxonomy - Because of the diversity of the insect complexes found on conifers in North America and the difficulty in differentiating among closely related species, taxonomists have played an important role in cone and seed insect research. Groups of particular significance are the cone beetles, Conophthorus (Wood 1982); the seedworms, Cydia (Heinrich 1926, Miller 1959, 1986b, 1987), the Dioryctria (Heinrich 1956, Mutuura and Munroe 1979, and Mutuura and Neunzig 1986); the coneborers, Eucosma (Heinrich 1923, Powell 1968) and the cone midges, Cecidodmyiidae (Gagne 1989). Unfortunately, distinctive morphological characters are vague or lacking for many species within these groups. By combining classical taxonomic techniques with new approaches such as pheromone response (Hanula et al. 1984a), isozyme analysis (Richmond 1988), and cuticular hydrocarbon analysis (Haverty and Page 1989) it should be possible to futher clarify species relationships.

CONE AND SEED INSECT PEST MANAGEMENT

Impact of cone and seed insects - In natural forest stands, where good and poor cone crops often occur in 2 or 3 year cycles, cone crop size is a major factor in regulating populations of cone and seed insects (Mattson 1971, 1980; Hedlin 1964; Shea 1989). Often, a delayed density dependent relationship exists between annual cone crop size and insect population. Populations tend to increase when good cone crops occur for 2 or more consecutive years, and crash in years when few cones are intitiated. This natural regulating mechanism is circumvented in seed orchards, where the goal is to sustain maximum annual seed production. Such cultural practices as wide tree spacing, fertilizer application, girdling, and plant hormone application are designed to provide large seed crops.

Integrated pest management in seed orchards is essential for achieving that goal (DeBarr 1971, 1981; Cameron 1981). Without it, cone and seed insects often destroy 50% or more of the crop (Fatzinger et al. 1980, Schowalter et al. 1985). Cone crop life tables are used extensively to determine the relative impact of each pest in a species complex and measure cone crop production efficiency (DeBarr and Barber 1975, Yates and Ebel 1978, Fatzinger et al. 1980, Rauf et al. 1981). Radiography is commonly used to assess seed damage, and is particularly useful for detecting late-season seed bug feeding (DeBarr 1970) and infestations of Megastigmus spp. (Schowalter et al. 1985). It is an integral part of cone analysis (Bramlett et al. 1977), which provides a method for estimating seed potential and seed efficiency. Life tables, radiography, and cone analysis are combined in an inventory monitoring system for seed orchards (Bramlett and Godbee 1982). Particularly challenging is assessing the impact of transient

insects that produce few easily detected symptoms of damage (Koerber 1963, DeBarr 1967) but destroy immature seeds (Krugman and Koerber 1969, DeBarr and Ebel 1974) and cause conelet abortion (DeBarr and Ebel 1974, DeBarr and Kormanik 1975, Rauf et al. 1984, Schowalter 1986). Individual trees of a species almost always differ greatly in inherent susceptibility to infestation by cone and seed insects (Merkel et al. 1965, Merkel 1967b). These differences are particularly evident in clonal seed orchards (DeBarr et al. 1972, Schowalter and Haverty 1989). Little is known about how these insects locate their hosts (Mattson et al. 1984), but monoterpenes appear to affect oviposition (Hanula et al. 1985). Fortunately, there is little or no correlation between susceptibility to cone and seed insects and growth (Askew et al. 1985a, 1985b). Although forest geneticists are not interested in breeding trees resistant to cone and seeds, it is possible to take advantage of inherent differences among trees in experimental designs for research, using highly susceptible trees as "indicator trees" or by identifing susceptible clones or families and concentrating control efforts on those most vulnerable to attacks (DeBarr 1971, 1981; DeBarr et al. 1972).

"Do I need to control the pest?" - This is the first question a seed orchard manager asks. Integrated pest management requires methods for predicting the need for control. Because cone and seed insects are often hidden in the host or soil, are nocturnal, or cause significant losses at relatively low population levels, most research has quantified damage rather than insect numbers. Monitoring damage provides data on relative impact on seed production, or what I call a "post-mortum" on a seed crop. Use of crop life-tables quantifies seed losses over time and identifies chronic pest problems at a given location. But such data are of limited value in predicting insect populations and subsequent losses. To go from a preventative to a suppressive approach, methods for monitoring insect populations must be developed.

Blacklight traps were used extensively by researchers in the Southeastern U.S. to monitor lepidopterous cone and seed insects (Merkel and Fatzinger 1971, Yates and Ebel 1975, Cameron 1981), but they lacked the specificity required for use by orchard managers. Researchers were able to demonstrate pheromone based behavior by cone and seed insects (Hedlin and Ruth 1968, Fatzinger and Asher 1971, Kinzer et al. 1970, Fatzinger 1972, DeBarr and Berisford 1981) and response to synthetic chemical attractants (Weatherson et al. 1977). It has only been recently, however, that sex pheromones for a number of important cone and seed insects were identified by electroantennogram (EAG) bioassays of male antennae and field screening of synthetic sex attractants. These include the seedworm moths, Cydia spp. (DeBarr et al. 1984, Grant et al. 1989, Katovich et al. 1989) and the coneworm moths, Dioryctria spp. (Meyer et al. 1982, 1984, 1986; Grant et al. 1987). Two factors are clearly evident from these studies. First, cone and seed insects produce (Meyer et al. 1986; Grant et al. 1987) and respond to very low amounts of pheromone (Meyer et al. 1984, Grant et al. 1989. Second, traps must be placed in

the tops of tree crowns to be effective (DeBarr and Berisford 1981, Hanula et al. 1984c, Grant et al. 1989). Pheromones offer several possible uses in seed orchard pest management (DeBarr et al. 1984). These include detecting infestations, monitoring population trends, predicting potential losses, timing control tactics, and direct control strategies (DeBarr et al. 1984). Since 1981, traps baited with synthetic attractants have been used in southern pine seed orchards to monitor populations of four Dioryctria spp. (Hanula et al. 1984, Weatherby et al. 1985). This trapping has been most useful in providing an "early warning" for D. disclusa Heinrich (DeBarr et al. 1982a). Progress toward integrated pest management in Douglas-fir seed orchards has been greatly advanced by the development of damage prediction based upon egg counts of the Douglas-fir cone gall midge, Contarinia oregonensis Foote (Miller 1986a) and the Douglas-fir cone moth, Barbara colfaxiana (Kearfott) (Sweeney and Miller 1989).

"When is the best time for control?" - This is the second question a seed orchard manager asks. Timing control tactics to coincide with periods when insects are most vulnerable can increase effectiveness and cut costs. Optimum treatment times can be keyed to host phenology or predicted by degree-day models, which are based upon insect development in relation to temperature. For example, orchard managers in the Southeastern U.S. have a 7-day "window of opportunity" in which to prevent cone attacks by D. disclusa (DeBarr and Barber, unpublished). To be effective, sprays must be applied to kill larvae feeding in catkins before they initiate attacks on cones.

Degree-day models have been developed to predict optimum spray dates for each generation of the Nantucket pine tip moth, Rhyacionia frustrana (Comstock) (Garguillo et al. 1984). These models are now being used in conjunction with a Remote Automated Intelligence Network (RAIN), an electronic communication and data retrievial system which links together field personnel, extension specialists and researchers (Pickering et al. 1989a, 1989b). Research is underway to develop similar models for several other cone and seed insects, including D. amatella (Hanula et al. 1984b, Hanula et al. 1987), L. corculus and T. bipunctata (Nord and DeBarr, unpublished), which can be used on the RAIN system.

"How do I control the pest?" - This is the third question a seed orchard manager asks. With few exceptions, cone and seed insects are controlled with chemical insecticides in seed production areas and seed orchards. Insecticides are implanted into stems or applied by ground equipment or aircraft. Both residual and systemic insecticides have been used, almost always on a preventative basis to protect crops from attacks that are anticipated. Two insecticides, azinphosmethyl (Guthion®) and dimethoate (Cygon®) have been used in seed orchards for more than 20 years (Johnson 1962, 1963b, 1963c; Merkel 1962, 1964; Merkel and Yandle 1965; Buffam and Johnson 1966). During the mid-1970's a large cooperative effort was undertaken to find other insecticides suitable for use in southern pine seed orchards (van

Buijtenen 1981). Laboratory tests were conducted to find insecticides highly toxic to L. corculus (DeBarr and Nord 1978) and D. amatella (DeBarr and Fedde 1980). Several of these insecticides with low mammalian toxicities, and minimal environmental hazards were then field tested (DeBarr 1978, Nord et al. 1984, 1985). Additional research has shown that these same insecticides can be used in other regions of North America (Rauf et al. 1982, Haverty et al. 1986, Rush et al. 1987).

Most insecticides used in southern pine seed orchards are aerially applied (Barry et al. 1984), while application by ground equipment is still common in other regions of North America. Aerial applications provide more timely applications and better spray coverage in the tops of tall trees, which results in better protection of seed crops. Other advantages include lower application rates, smaller spray volumes, less environmental contamination, lower impact on populations of nontarget organisms, reduced worker exposure, and lower costs.

Systemic insecticides, which translocate within forest trees, are highly effective for controlling many cone and seed insects. Some are applied to foliage, some to soil and some as trunk implants (Johnson and Rediske 1965, Hedlin 1966, Johnson and Zingg 1967, Merkel and DeBarr 1971, DeBarr 1978, Summers and Miller 1986, and Stein et al. 1988). They work best on insects attacking rapidly growing parts of the tree, such as developing needles, terminals, or elongating cones. Cone and seed insects that feed on needles prior to attacking cones or whose feeding periods coincide with rapid cone development in the spring are highly vulnerable. Examples, include early stage nymphs of L. corculus, which feed on pine needles and can be killed by accumulated residues of acephate or carbofuran (DeBarr, unpublished) and spruce budworm larvae, Choristoneura fumiferana (Clemens), which are vunerable when they mine needles prior to attacking cones (Hedlin et al. 1980). Soil applications provide extended uptake, if adequate rainfall occurs, but relatively large doses of insecticide per tree are needed for control (DeBarr 1978, DeBarr et al. 1982). Foliar applications have shorter periods of effectiveness than either soil applications or stem implants, and have application problems similar those associated with non-systemic insecticides. Stem implants require the least amount of insecticide per tree and greatly reduce environmental risks and impact on natural enemies, but are labor intensive, and therefore expensive. Stem implants are effective against many different groups of cone and seed insects and individual tree stem implants have been widely used for cone and seed insect control throughout North America, except in the Southeastern United States. In the southeast, the labor costs are considered excessive for treating the large numbers of trees that must be protected and oleoresin exudation in pines reduces the effectiveness of commercially available delivery devices (DeBarr, unpublished).

Alternatives to chemical control - Unlike most forestry situations, there are numerous research opportunities for developing

alternatives to chemical control in seed orchards because of the high value placed upon genetically improved seeds. Examples include the use of prescribed fire to control Conophthorus beetles that overwinter on the forest floor (Miller 1978, DeBarr and others, unpublished) or cold water misting to force Douglas-fir flower development out of phase with the attack period for C. oregonensis (Miller 1983). Use of microorganisms such as fungi (Timonin et al. 1980) or bacteria (McLeod and Yearian 1981, Fogal 1986, Cameron et al. 1987) also has potential. Locating orchards just outside the natural species range or in predominately agricultural areas appears to offer advantages from both the pest management and genetic viewpoint. Such orchards would be less likely to become infested and infestations could most likely be eradicated if they did occur. In addition, since background pollen would be greatly reduced or eliminated, genetic gains would also be enhanced. Sanitation will also work for some pests. Cydia spp., which overwinter in the axis of mature cones, are usually removed from the orchard at cone harvest.

Behavioral chemicals also offer promise for controlling cone and seed insects. We have recently shown that male D. disclusa are unable to locate baited traps in orchards permeated with synthetic pheromone (DeBarr et al., unpublished), which suggests that it may be feasible to use mating disruption in seed orchards. However, it remains to be shown that attacks can be reduced, particularly if there is a large influx of gravid, mated female moths from surrounding stands. Little is known about migration of cone and seed insects, but it has important implications for the use of such strategies as trapping all local males or male disruption.

If it is difficult to study cone and seed insects, it is even more so to study their natural enemies. Not much is known about the natural enemy complexes for most cone and seed insects. Yates (1989) has compiled a list of more than 1000 natural parasitoids or predators of cone and seed insects. Natural enemies of the white pine cone beetle are rare (DeBarr, unpublished, Godwin and Odell 1965). In contrast, D. amatella has an array of parasites (Belmont and Habeck 1983), but their role in regulating populations is unclear. Egg parasites seem to be the best candidates for use in seed orchards to mitigate cone and seed insect populations. Trichogramma spp. have been observed parasitizing Dioryctria eggs (DeBarr, unpublished), Bustillo 1983) and three species of egg parasites frequently attack feral eggs of L. corculus in the Southeastern U.S. (DeBarr 1979). Inundative or augmentative releases of these natural enemies may be feasible in some seed orchards.

RESEARCH BENEFITS FOR APPLIED TREE IMPROVEMENT

Weir (1975) pointed out that "the impact of cone and seed insects on intensive forest management efforts is nearly invisible to all but the tree improvement practitioner," but that the value losses in the absence of effective controls is comparable to the

destruction caused by the southern pine beetle, Dendroctonus frontalis Zimm. In 1987 almost 126 tons of genetically improved seeds were produced in the Southern U.S. (Jett 1988). They were used to grow more than 1.6 billion seedlings for reforesting 2.5 million acres, 74% of the acreage planted in the U.S. (Lantz 1988). Almost 11% of the production by the North Carolina State University-Industry Cooperative was from second-generation seed orchards (Anonymous 1989). This production would not have been possible without cone and seed insect control.

SUMMARY

Past research has provided considerable knowledge on insects attacking cones and seeds of forest trees in North America. Current research on these insects in remote regions or less widely distributed tree species continues to broaden our knowledge. Research is also directed at providing more detailed information on biologies and behavior of major pest species. This information is essential for progress in pest management. Many opportunities exist for future research on cone and seed insects. Basic research is needed in such areas as insect biology, diapause, migration, population dynamics, and taxonomy. With additional knowledge, applied research can lead to new pest management techniques for predicting damage and optimum control times, as well as new control tactics and strategies based upon the use of behavioral chemicals, biocontrol, or silviculture.

Cone and seed insect research is unique in that its importance is relatively recent. If alternative methods of propagation, such as rooted cuttings (Frampton and Hodges 1989) or tissue culture (Hanover 1987), finally become commercially practical, they could displace seed production. In that case, cone and seed insects would lose their "pest status," and revert to being only of academic interest. However, until such changes come about, research on cone and seed insects is vital to ensure the continued success of applied forest tree improvement programs throughout North America.

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CONE AND SEED DISEASES OF CONIFERS IN CANADA

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ABSTRACT

The recent developments of seed orchards, tree improvement programs and production of container-grown forest nursery seedlings has made us aware of the importance of cone and seed diseases. This paper reviews the biology, life history, damage and management of the most important of these diseases in Canada: inland spruce cone rust [Caloscypha fulgens (Pirs Boud.)], the seed or cold fungus, Sirococcus blight, and Fusarium and other seed-borne fungi.

RÉSUMÉ

L'apparition récente des vergers à graines, de programmes sur l'amélioration génétique des arbres et de la production en pépinières forestières de semis en récipients nous a fait réaliser l'importance des maladies des cônes et des graines. Le présent article porte sur la biologie, l'évolution, les effets et le traitement des plus importantes de ces maladies au Canada; rouille des cônes de l'épinette, maladie des graines ou des semis [Caloscypha fulgens (Pirs Boud.)], brûlure des pousses Sirococcus, infections Fusarium, et autres mycoses des graines.

INTRODUCTION

A discussion of conifer cone and seed pests must rightfully include information on cone and seed diseases. Although such diseases have been known for many years it is only in the past decade or so that their true importance has been appreciated. Two technological advancements in reforestation have brought about this recognition. The first of these is the establishment of ever-increasing numbers of seed orchards for production of genetically improved seed. Orchards produce high quality, but costly seeds which justify protection from diseases and other impediments. Accessibility of the seed orchard crop, as opposed to limited accessibility in the forest, also allows implementation of cultural and pest management practices to minimize disease-caused cone and seed losses. To date, in Canadian seed orchards, cone diseases have received more attention than seed diseases, but this emphasis could change as successful practices are worked out for cone diseases. A second technological change, i.e., production of container-grown seedlings, has demonstrated the importance of seed-borne pathogens. Each year production of such seedlings accounts for a larger share of the forest tree seedling production in Canada. There are several reasons why seed-borne pathogens are more evident in container nurseries than in traditional bareroot (open field) nurseries: (i) the growing medium is normally pathogen-free so diseases are more easily traced to seed-borne pathogens; (ii) definite numbers of seeds are sown in each growing cavity so germination reduction is more evident; (iii) the confined growing area of container nurseries results in closer scrutiny; and (iv) losses from seed-borne diseases are less likely to be masked by an array of other factors such as inclement weather, insects and birds.

The discussion here is limited to cone and seed diseases considered to be important and likely to be encountered in Canada. The biology, life history, damage and management are described for inland spruce cone rust, other cone rusts, the seed or cold fungus, Sirococcus blight and then, briefly, Fusarium and other seed-borne fungi. A more in-depth coverage with extensive illustrations of these and other cone and seed diseases of North America conifers is given in Sutherland et al. (1987). The reader should consult Sutherland (1985) regarding other diseases of seed orchard trees, such as root rots, that may affect cone and seed production.

INLAND SPRUCE CONE RUST

Inland spruce cone rust, Chrysomyxa pirolata Wint., is the most serious disease affecting spruce, Picea spp., cones (all species country-wide). Losses can be severe on both forest (Ziller 1974) and seed orchard trees (Sutherland 1985). High risk areas are those where spruces and the rusts' non-conifer hosts (alternate hosts) occur in abundance and in close proximity. A similar rust, coastal spruce cone rust, C. monesis Ziller, affects

Sitka spruce, Picea sitchensis (Bong.) Carr., cones on the Queen Charlotte Islands, British Columbia. The limited risk area and subtle differences in spore morphology are the main characteristics distinguishing this rust from C. pirolata.

The life history of C. pirolata is complex (Fig. 1). The rust is heteroecious (completes its life cycle on two unrelated plants) and has several spore stages. Alternate hosts, small and herbaceous to woody plants, of the genus Pyrola (wintergreens) and single delight [Monesis uniflora (L.) Gray] are often abundant as forest ground cover. The fungus is annual and systemic in spruce cones and perennial and systemic in the alternate hosts, at least in Pyrola asarifolia Michx. where it occurs throughout the plant including the rhizomes (Sutherland et al. 1984). The various spore stages, hosts on which they occur and time of occurrence are given in Figure 1.

Symptoms (host appearance) of cone rust are quite conspicuous in mid- to late-summer when diseased cones become light brown, dry out and open prematurely, liberating masses of yellow-orange spores (aeciospores). In contrast healthy cones are green at this time. Symptoms on rust-affected alternate host plants varies from no apparent effect on P. secunda L. to P. asarifolia in which plants atrophy over the years and have leaves that are more upright, and duller to chlorotic, than healthy plants. On spruce cones, signs (pathogen appearance) first appear soon after infection and consist of sticky, light, honey-colored ooze that develops on cone scales. Two to four weeks later, masses of powdery, yellow-orange aeciospores are released from diseased cones. These wind-borne spores result in infection of alternate host plants (Fig. 1). In the spring, coinciding with the time of spruce cone pollination, rust pustules develop on the undersurface of alternate host leaves and eventually release wind-borne basidiospores which infect spruce cones when they are upright and open for pollination. Uredinospores may also be released from the undersurface of alternate host leaves in spring through autumn (depending on the alternate host species). They infect other alternate host plants, i.e. they spread and intensify the pathogen on the non-conifer host.

During years when cone rust is severe the majority of the cones in a forest area or seed orchard can be ruined. Diseased cones produce few or no seeds and production of copious amounts of resin makes seeds difficult to extract. Also, seeds from diseased cones may also germinate abnormally. For these reasons, diseased cones should not be collected as they drastically lower seedlot quality.

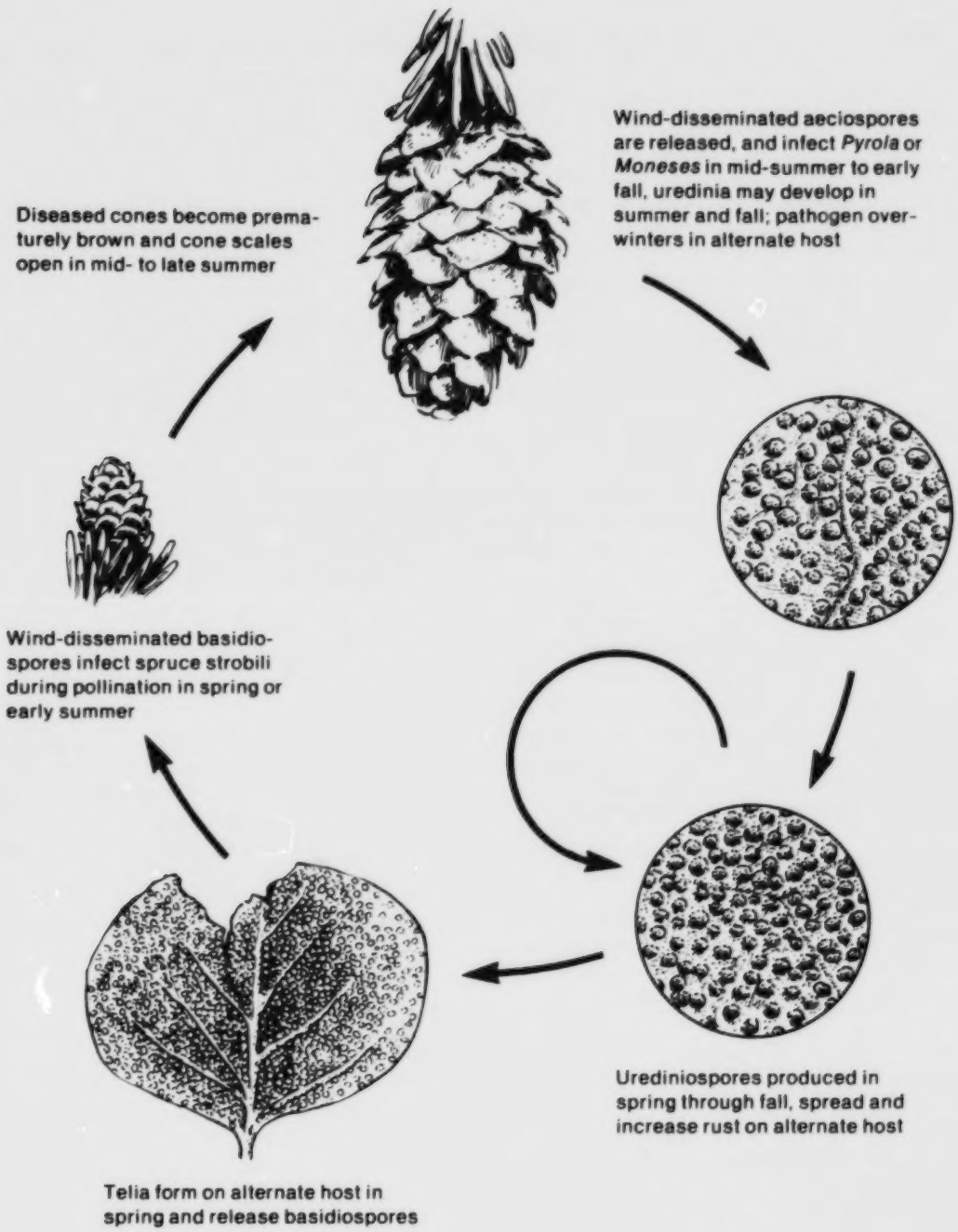
Wind-disseminated aeciospores are released, and infect *Pyrola* or *Moneses* in mid-summer to early fall, uredinia may develop in summer and fall; pathogen overwinters in alternate host
Diseased cones become prematurely brown and cone scales open in mid- to late summer
Wind-disseminated basidiospores infect spruce strobili during pollination in spring or early summer
Urediniospores produced in spring through fall, spread and increase rust on alternate host
Telia form on alternate host in spring and release basidiospores

Fig. 1. Life history of inland spruce cone rust, Chrysomyxa pirolata (from Sutherland et al. 1987).

As already demonstrated in British Columbia, the importance of spruce cone rust will increase across Canada as spruce seed orchards come on stream. Also, as shown in British Columbia, the best way to beat the problem (where no other complications exist) is to locate seed orchards in areas that are free of the alternate host. For example, southern interior British Columbia spruce orchards at Salmon Arm, where infected alternate hosts abound, can suffer cone losses of up to 60%. In contrast, orchards about 50 km south at Vernon, which is free of Pyrola because of the drier climate, have no cone rust. When orchards must be located in high risk areas, the cones must be protected by applying fungicides such as ferbam which is very effective against the disease (Summers et al. 1986). Newer systemic fungicides such as triadimefon appear to be as effective and perhaps less costly as fewer sprays are needed. Attempts to eradicate alternate host plants are probably futile as the basidiospores which infect cones are likely wind-borne for great distances. However, the alternate host plants are quite susceptible to fire so collecting cones from forests that have experienced recent, widespread fires may be worthwhile.

OTHER CONE RUSTS

Other rusts such as Chrysomyxa woroninii Tranz. and American spruce-raspberry rust, Pucciniastrum americanum (Farl.) Arth., which occur on spruce needles or buds may also affect spruce cones. The latter fungus has been shown to drastically reduce both the seed content and germination of seeds from affected cones (Smith et al. 1986). However, to date no management recommendations have been developed for these diseases.

SEED OR COLD FUNGUS

The seed or cold fungus, Caloscypha fulgens (Pers.) Boud., acquired its name because it is seed-borne and it can grow fairly well at low temperatures. It was first found affecting seeds in Ontario bareroot nurseries (Epners 1964) and subsequently it was detected in Great Britain on conifer seeds imported from western North America (Salt 1974). Assays of stored seeds in British Columbia confirmed its presence there (Sutherland and Woods 1978). In 1989, low levels of the fungus were found in spruce seeds from Nova Scotia (J.R. Sutherland, unpublished data). Presence of the fungus on seeds from western, central and eastern Canada indicates that it occurs throughout the country.

Caloscypha fulgens is a large fairy cup fungus that inhabits forest litter and seeds acquire the fungus when cones contact infested litter. Therefore, seeds from squirrel caches or cones collected from the forest floor are most likely to contain the fungus. Experiments in British Columbia (Sutherland 1981) showed that the percentage of seeds infected increased steadily after cones were in contact with infested litter for a period of between

2 and 8 weeks. In contrast, seedlots originating from cones picked from recently felled logging slash or standing trees (forest or seed orchard) do not harbor the fungus. Also, seedlots of conifers with serotinous cones do not have the fungus. Assays of stored seeds in British Columbia revealed that about 30% of the spruce seedlots, and lesser amounts of Abies spp. and Douglas-fir, Pseudotsuga menziesii (Mirb.) Franco, seedlots, have 1 to 30% of the seeds which yield the fungus. Besides these species, seeds of many other conifers are susceptible. Low incidence of the fungus is often thought to be inconsequential, but this is not true because the fungus spreads during stratification, afterward in pre-sowing storage, and again in seedbeds and multiple-sown container cavities. The low temperatures and dry conditions used for long-term seed storage prevent its spread.

Seed assay techniques have been developed for C. fulgens (Sutherland 1987). Also, when abundant the fungus can be seen as hard masses of whitish mycelium on seedcoats or as mycelium on seeds following stratification. Another clue to the presence of this fungus is that infested seedlots may germinate poorly if stratified.

The pathogen kills seeds prior to germination. Once germination begins germinants are immune, i.e., it causes a pre-emergence damping-off. However, unlike other such damping-off fungi it mummifies rather than rots the seed contents. Although both sexual and asexual spores are produced, their role in disease development appears to be in fungus dissemination rather than in infection. Figure 2 gives the life history of C. fulgens.

Prevention is the best way to control this problem. Collection of cones from squirrel caches and the forest floor should be restricted. If such cones are collected, spread of fungus can be minimized by proper drying of cones in cone drying sheds and by not storing wet cones for prolonged periods at cool temperatures. Infested seedlots should be stratified for as short a time as possible and sown immediately afterward. If seeds are stored after stratification they should be kept at 1 to 2°C. Adding a fungicide to the stratification water will prevent the fungus spreading during stratification and a fungicide dusting of seeds before sowing may also be used. Since cool, wet conditions favor the disease, and cool temperatures slow seed germination, infested seedlots should only be sown after seedbed soils are warm or containers are artificially warmed. In bareroot nurseries two other sources of inoculum can exist, i.e. infested seeds from previous nursery crops (conifer) and infested forest litter used to amend soil organic matter.

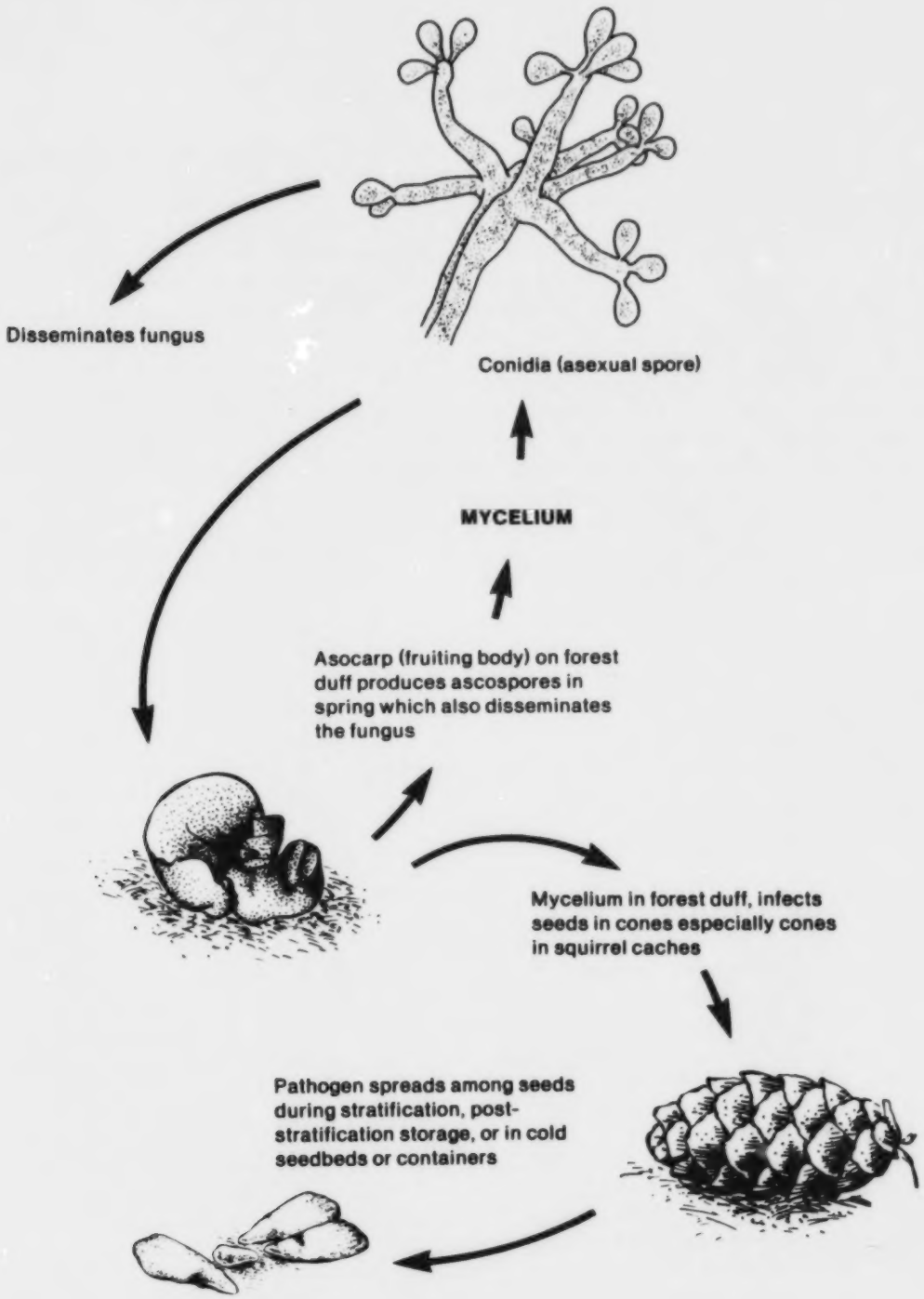
Disseminates fungus
Conidia (asexual spore)
MYCELIUM
Asocarp (fruiting body) on forest duff produces ascospores in spring which also disseminates the fungus
Mycelium in forest duff, infects seeds in cones especially cones in squirrel caches
Pathogen spreads among seeds during stratification, post-stratification storage, or in cold seedbeds or containers

Fig. 2. Life history of the cold or seed fungus, Caloscypha fulgens (from Sutherland et al. 1987).

SIROCOCCUS BLIGHT

This disease is caused by the fungus Sirococcus strobilinus Preuss, a seed-borne pathogen of container-grown seedlings. Sirococcus blight of forest trees (especially regeneration) and bareroot nursery seedlings results from wind- and rain-borne inoculum. Although possible, the probability of seed-borne inoculum resulting in disease of forest trees and bareroot nursery seedlings is small. Conditions are ideal in container nurseries for disease outbreaks originating from seed-borne inoculum, e.g., sowing of several seeds (in close proximity) per container cavity and sowing into a non-soil medium which allows spread of the fungus among seeds. Frequent periods of low light intensity in container nurseries may also enhance Sirococcus blight. Most seeds containing S. strobilinus have shriveled contents and do not germinate. In containers, the fungus is thought to grow from an infected to a healthy seed, which acquires the fungus and becomes diseased after germination (Fig. 3). From these disease centers secondary spread occurs by spores in splashing irrigation water.

In container nurseries Sirococcus blight kills germinants and young seedlings in early spring to early summer. Needles are killed from the base upward; dead seedlings remain upright and bear the small black fruit bodies of S. strobilinus. Since the pathogen is seed-borne, incidence and severity of diseased seedlings varies among seedlots. Sirococcus blight also affects bareroot seedlings, but symptoms usually appear in late summer to early fall and are confined to specific portions of the needles and stems of the shoot.

Sirococcus blight management on container-grown seedlings, where it is most severe, is achieved by using fungicides and modifying cultural practices (Sutherland et al. 1989). Adding a fungicide to the seed stratification water is helpful as are fungicide sprays starting at the first appearance of disease symptoms. Spraying must be done often to protect the rapidly growing seedlings. Reducing humidity by regulating irrigation and improving air ventilation is worthwhile. In nature the fungus can frequently be found on the previous year's spruce cones. These cones contain seeds with a high incidence of S. strobilinus and are probably the source of the pathogen in seedlots. Such cones are frequently inadvertently included in cone collections. Seedlots from seed orchards do not contain the pathogen as cones there are picked every year.

FUSARIUM AND OTHER SEED-BORNE FUNGI

Although earlier studies (see references cited by James 1985) showed that species of Fusarium were seed-borne, the advent of container nurseries where losses from seed-borne fungi are more easily documented renewed interest in these fungi in both container and bareroot nurseries. In North America, James (1985) has been instrumental in determining the identity, biology and

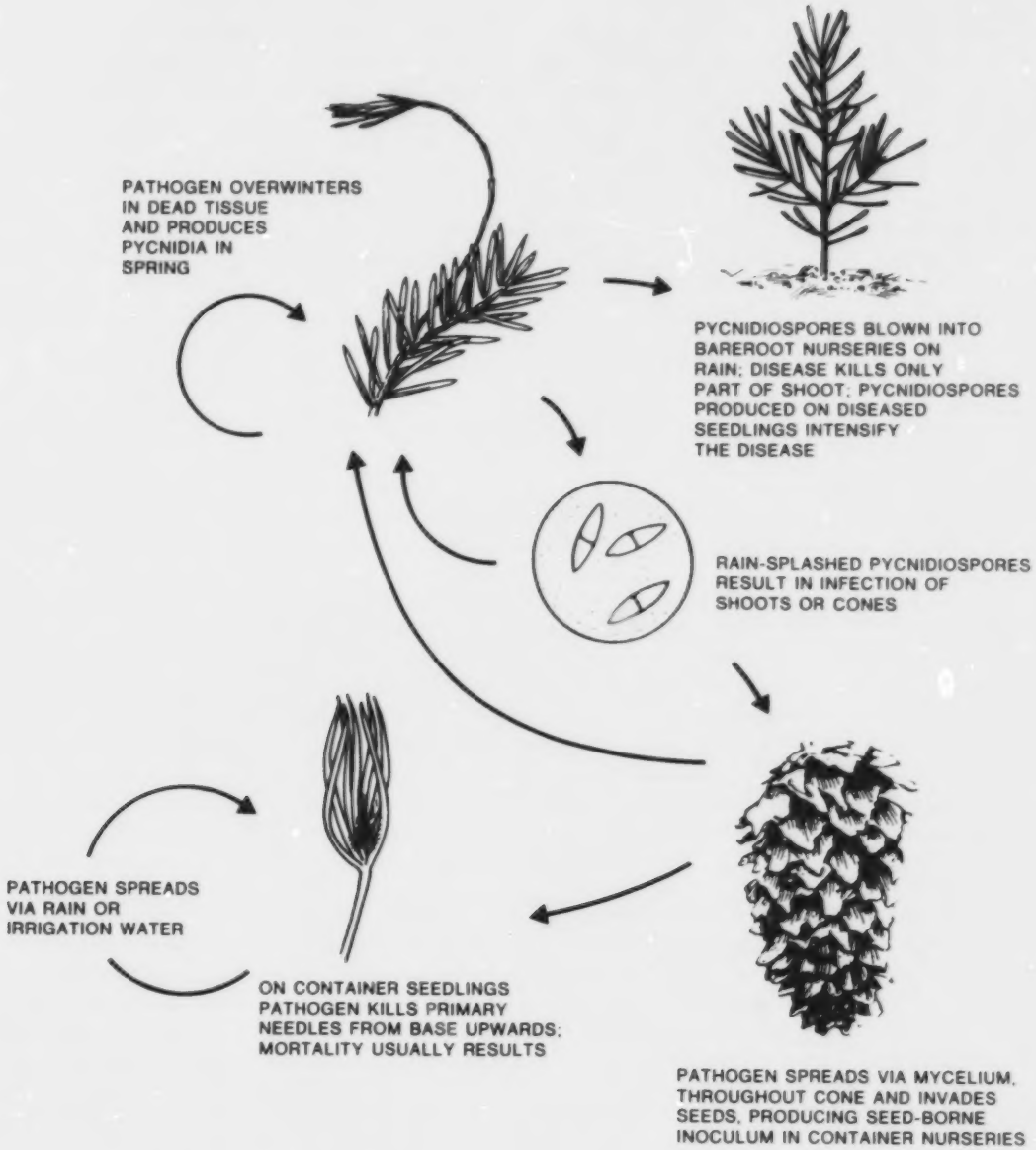
PATHOGEN OVERWINTERS IN DEAD TISSUE AND PRODUCES PYCNIDIA IN SPRING
PYCNIDIOSPORES BLOWN INTO BAREROOT NURSERIES ON RAIN; DISEASE KILLS ONLY PART OF SHOOT; PYCNIDIOSPORES PRODUCED ON DISEASED SEEDLINGS INTENSIFY THE DISEASE
RAIN-SPLASHED PYCNIDIOSPORES RESULT IN INFECTION OF SHOOTS OR CONES
PATHOGEN SPREADS VIA RAIN OR IRRIGATION WATER
ON CONTAINER SEEDLINGS PATHOGEN KILLS PRIMARY NEEDLES FROM BASE UPWARDS; MORTALITY USUALLY RESULTS
PATHOGEN SPREADS VIA MYCELIUM THROUGHOUT CONE AND INVADES SEEDS, PRODUCING SEED-BORNE INOCULUM IN CONTAINER NURSERIES

Fig. 3. Life history of Sirococcus blight, Sirococcus stroblinus (after Sutherland et al. 1989).

pathology of seed-borne fusaria. Much still needs to be done on this diversified group of fungi, but it is now known that they can cause pre- and post-emergence damping-off, root rots and top blights of conifer seedlings (James 1985). Fusarium oxysporum Schlect. is the species most often isolated from seeds, followed by F. solani (Mart.) Appel & Wr. Other fusaria occurring on conifer seeds are F. moniliforme Sheldon and F. roseum (Lk.) Sacc. James (1985) suggests that seeds probably acquire Fusarium when cones or seeds contact infested soil; seedlots from squirrel caches also contain large populations of fusaria and other fungi. Until more information is available on the biology, pathogenicity and other characteristics of seed-borne fusaria it is difficult to make management recommendations. Present efforts in British Columbia and the western United States (Dumroese et al. 1988) are concentrating on sterilization techniques for ridding conifer seeds of fusaria.

A wide variety of "molds" have been isolated from seeds of numerous conifer species (e.g. Mittal and Wang 1987; Richardson 1979). At present, the general consensus is that most of these fungi are at best only weakly pathogenic, but some such as Botrytis cinerea Pers. (Mittal et al. 1987) can kill germinants and young seedlings and cause shoot diseases (gray mold) of older seedlings.

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THE TAXONOMY, LIFE HISTORY AND CONTROL OF *CONOPHTHORUS* (COLEOPTERA: SCOLYTIDAE) IN EASTERN NORTH AMERICA

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ABSTRACT

The cone beetles in the genus Conophthorus Hopkins (Coleoptera: Scolytidae) are serious pests of many species on pines in North America. In eastern North America, three species are recognized, C. resinosae Hopkins, C. banksianae McPherson, and C. coniperda (Schwarz). The beetles are very difficult to identify on the basis of morphological characters, and more taxonomic study is needed to verify the number of species in the genus. The females initiate attack on the cones, which are completely killed. Larvae feed on seeds and on cone tissue. These beetles are univoltine. Control of the beetles can be achieved by removal of the infested cones on the ground in the fall or in the spring before emergence, or by systemic and contact insecticides. The known parasites and predators of the species are listed, and the various control strategies are discussed.

RÉSUMÉ

Les scolytes des cônes, du genre Conophthorus Hopkins (Coleoptera: Scolytidae), causent des dommages importants à plusieurs espèces de pins en Amérique du Nord. A l'est du continent, on a identifié trois espèces de scolytes: C. resinosae Hopkins, C. banksianae McPherson, et C. coniperda (Schwarz). Il est très difficile d'identifier ces coléoptères par leurs caractères morphologiques et seules d'autres études taxonomiques pourront confirmer le nombre d'espèces que compte le genre. Ce sont les femelles qui attaquent les cônes, les tuant complètement. Leurs larves se nourrissent des graines adhérant aux tissus du cône. Ces coléoptères sont univoltins. On peut les réprimer en enlevant du sol les cônes infestés, soit à l'automne, soit au printemps avant leur émergence, ou encore en recourant à des insecticides systémiques et à des insecticides de contact. Le présent article présente aussi une liste des parasites et des prédateurs connus de ces espèces et examine les diverses méthodes de lutte.

INTRODUCTION

The genus Conophthorus Hopkins is comprised of 15 species (Wood 1982; Flores and Bright 1987) found only in North America. Three species, the white pine cone beetle, C. coniperda (Schwarz), the red pine cone beetle, C. resinosae Hopkins and the jack pine tip beetle, C. banksianae McPherson are found in eastern North America. The first two species are serious pests of cones. In some years they can destroy 90-100% of the crop (Hedlin et al. 1980 and references therein). The jack pine tip beetle, as its common name suggests, feeds on the tips of jack pine shoots, but does not feed on cones (McPherson et al. 1970a,b).

In general, the species of Conophthorus are very difficult to distinguish on the basis of external features, and often the host species is used for species determination. Therefore other taxonomic characters are needed to aid species identification and to confirm the presence of sibling species. Correct identification, and an understanding of the biology of Conophthorus species, are also essential for the development of pest management programs. With the significant expansion of tree improvement in North America, and the concomitant establishment of seed orchards, the economic importance of the cone beetles as pests is expected to increase.

This paper reviews the taxonomy, life history, and control of the three eastern species of Conophthorus.

TAXONOMY

The first published observations of Conophthorus were in a report by Packard (1890) who listed the observations by W.H. Harrington (in correspondence) of "Dryocoetes affaber (?)" adults and larvae in the cones of red pine, Pinus resinosa Ait. Later, Harrington (1891, 1902) published notes under the names D. affaber and D. autographus. Hamilton (1893) reported collecting cone beetles from white pine, P. strobus L., thinking them similar to the species identifed by Harrington as Dryocoetes, but questioning their identity as Dyrocoetes. Schwarz (1895) offered the first taxonomic description of the cone beetle attacking white pine and placed the species under the genus Pityophthorus Eichhoff. He indicated that this species (P. coniperda) differs from the generic description of Pityophthorus in the structure of the antennae and the anterior tibiae, but thought it premature to erect a new genus for an isolated species. He also noted that superficially this species was at once distinguishable from Pityophthorus by its larger size, less elongate form, and the structure of the elytral declivity.

Following the discovery that several other species of pines were infested with cone beetles, A.D. Hopkins (1915) erected Conophthorus as a new genus with C. coniperda as the type species.

He then distinguished Conophthorus from Pityophthorus by the absence of sutural septa in the antennal club. Wood (1982) distinguishes Conophthorus from Pityophthorus "... by the larger body size, by the stout body form, by the aseptate antennal club, by the pronotum that has an indefinite summit on the basal third, and the asperites continuing to or near the base in the lateral areas, and by the monogamous cone-infesting habit (with one exception)." However, the concept of Conophthorus as a distinct genus is questionable (Wood 1982). Although the genus does contain a distinctive species group, this may be nothing but a species group or subgenus of Pityophthorus. Flores and Bright (1987) note the dilemma of separating these genera in the species C. terminalis Flores and Bright.

Hopkins appears to have been obsessed with host selection by insects, so much so that it is reflected in his descriptions of new species; he described 14 new species of Conophthorus, all after their host plants. The number of species of Conophthorus recognized by Hopkins has been reduced by Wood (1977) who, by using external anatomical characters, synonymised C. virginae Hopkins with C. resinosae, declared C. clunicus Hopkins and C. taeda Hopkins synonyms of C. coniperda, and placed six of Hopkins's western species under synonomy with C. ponderosae. New species of Conophthorus have been recognized (Wood 1982; Bright and Flores 1987), bringing the present day total back to 15. The most recent key to the species uses the structural features of the elytra and pronotum, but the separation of some species by anatomical characters is extremely difficult because the diversity of characters is limited, variable, and poorly developed (Wood 1982). Thomas (1957, 1967, 1971) examined the external anatomy of larvae and pupae, and the gastric caeca of larvae and adults of several Conophthorus spp., but found no consistent differences that would separate one species from another.

Two sibling species are recognized, C. banksianae and C. resinosae, (Wood 1982). The discovery of sibling species began when Thomas and Lindquist (1956) found adults of Conophthorus attacking the shoots of jack pine, Pinus banksiana Lamb., in 1952 in Ontario. Herdy and Thomas (1961) conducted a brief study of the beetles' biology, and Herdy (1963, unpublished) found no anatomical character that would separate these beetles from C. resinosae. McPherson et al. (1970a,b) re-investigated the biology of C. resinosae and Conophthorus sp. on jack pine and described the latter as a new species, C. banksianae McPherson. Conophthorus banksianae, the jack pine tip beetle, was considered distinct from C. resinosae, the red pine cone beetle, because it appeared to be bivoltine, the adults were on average shorter and narrower, and eggs, larval and pupal stages were present longer in the field (McPherson et al. 1970a). Furthermore, the tip beetle fed only on shoots (those of jack pine, P. banksiana Lamb.; red pine,; scotch pine, P. sylvestris L.; or, ponderosa pine, P. ponderosa Laws.), and showed a preference for the shoots of jack pine (McPherson et al. 1970b). When exposed to the resins

of jack pine or red pine, the tip beetle was the most tolerant of jack pine resin. The red pine cone beetle was univoltine (Lyons 1956, McPherson et al. 1970a), attacked the cones and shoots of red and jack pine, and showed about equal tolerance for the resins of both trees (McPherson et al. 1970a,b). The validity of C. banksianae as a distinct species has been questioned (Wood 1982). Current research on life history, host acceptance behaviour, genitalia, karyotype, isozymes, and pheromones (unpublished data), and on cuticular hydrocarbons by Haverty et al. (1989) strongly suggests that C. banksianae and C. resinosae are the same species.

Additional biosystematic studies of Conophthorus is needed to clearly establish the number of species in the genera and the validity of the genera itself. One interesting and productive area for future research is on host acceptance behaviour. Mating occurs on, or in the host, and most of the species of Conophthorus appear to be specific to a single host. The C. ponderosae complex is the exception; however, but there may be sibling species in this group. An examination of the host-insect relationships should yield important information to further our understanding of the evolution of these beetles; such information would also be useful for their management.

LIFE HISTORY

The basic life history of the three eastern species of Conophthorus is reasonably well known from the studies of Lyons (1956) and McPherson et al. (1970a) for C. resinosae; Godwin and Odell (1965) and Morgan and Mailu (1976) for C. coniperda; and Herdy and Thomas (1961) and McPherson et al. (1970a) for C. banksianae. Other references can be found in de Groot (1986a).

Adult beetles emerge in the spring from brood cones (C. coniperda) or from shoots (C. resinosae and C. banksianae) on the ground. The females initiate attack on the cone or the shoot killing the entire structure. The first attacks are for feeding and mating, while oviposition occurs in subsequent attacks. Eggs are deposited singly in niches cut along the sides of a central gallery and are covered with frass and boring debris. Larvae feed for several weeks and pupate in the host tissue after the second instar. Callow adults of C. coniperda generally remain in the cone until the next spring, but some may emerge from the cone to bore into shoots to overwinter. Young adults of C. resinosae and C. banksianae emerge from the brood gallery to feed on shoots before overwintering. Both C. coniperda and C. resinosae are univoltine. McPherson et al. (1970a) believed that C. banksianae was bivoltine; however, recent work by de Groot (unpublished) corroborates the earlier work of Herdy and Thomas (1961) that C. banksianae is univoltine.

Several natural enemies of the three eastern species have been recorded. Hall and Wilson (1974) found that 15-40% of the

second-instar larvae and pupae of C. banksianae were attacked by Cecidostiba dendroctoni Ashmead (Hymenoptera: Pteromalidae). Two species of parasites, Eurytoma pini Bugbee (Hymenoptera: Eurytomidae) and Habrocytus sp. (Hymenoptera: Pteromalidae) were recovered from C. banksianae larvae by Herdy and Thomas (1961). Adults of Bracon rhyacioniae (Muesebeck) (Hymenoptera: Braconidae), a parasite, were found in red pine shoots containing larvae of C. resinosae (Lyons 1956). Predation by larvae of Attalus nigrellus (Leconte) (Coleoptera: Melyridae) caused 32% mortality of C. resinosae larvae, pupae, and immature adults in one year (Lyons 1956). Lyons (1956) found maggots of Lestodiplosis sp. (Diptera: Cecidomyiidae) attacking C. resinosae larvae in cones. Cephalonomia hyalinipennis Ashmead (Hymenoptera: Bethylidae) was reared by Godwin and Odell (1965) from C. coniperda. A braconid, Spathius sp., was also noticed by Godwin and Odell (1965) emerging from the cones infested with C. coniperda. Nematodes of Aphelenchoides sp. Fisher (Tylenchida: Nematodea) have been found within the bodies of C. coniperda (Godwin and Odell 1965). A fungus, Aspergillus niger Van Tieghem, has been implicated as causing mortality of C. coniperda (Godwin and Odell 1965), but it may be associated with moribund insects only.

CONTROL

The need for control will most likely be for C. coniperda. White pine is becoming an important part of the tree improvement program in several jurisdictions and is important to the future economy of many areas. Considering that C. coniperda can destroy the entire cone crop (Hedlin et al. 1980), the need to have available control methods for seed orchards or seed production areas is obvious. In comparison to white pine, red pine is generally less important as a species for reforestation (except for the reclamation of lands), and in economic value. At present, there is little interest in the improvement of red pine because the genetic variation is thought to be minimal (although there is renewed debate about this); therefore, a tree improvement program would not be cost-effective. Consequently, the need to control C. resinosae on red pine may only arise when seed is unavailable from local provenances or seed collection sites in a seed zone. The need to control C. resinosae on jack pine cones is, at present, not anticipated because the cones of jack pine are seldom attacked by this species (see deGroot 1986b and references therein). Attacks by C. banksianae on the tips of jack pine can reduce the number of available cones (de Groot 1986b); however, the need for control of C. banksianae will seldom be considered because populations have rarely been high enough or persistent enough to cause economic damage (personal observations).

An examination of the life cycle of Conophthorus reveals two windows of opportunity for control: when beetles are on the ground overwintering in cones or shoots, and when they emerge in the spring to begin mating and oviposition.

Miller (1915) suggested that the cones be raked up and burned in the fall. Miller (1978) and Mellish (1987) both evaluated a prescribed burn in red pine stands to control C. resinosae. They found that it could be used with some success provided that there was suitable weather for burning and that the beetles had not emerged. In this regard, burning in the fall appears to be advantageous.

Chemical insecticides for control of Conophthorus coniperda have been tried on several occasions beginning with the use of 6% DDT, dieldrin, malathion, and lindane by Godwin and Hastings (1956). They applied these insecticides with a mistblower when the beetles were emerging in the spring, but the applications were not effective as the whole cone crop was destroyed. Aerial applications of lindane or endrin at 1.1 kg ai/ha was also ineffective (Godwin and Hastings 1957). Hastings and Avery (1968) reported that aminocarb, dictrotophos, fenthion and mexacarbamate were highly toxic when applied topically to adults in the laboratory, and dicrotophos increased cone survival from 46 to 86% when implanted into the stems of the trees. Ehlers et al. (1978) found that a broadcast application of granular carbofuran to the mineral soil at 9 g AI/cm diameter of tree at 1.3 m (DBH) reduced cone damage by C. coniperda by 67 to 91 percent. Carbofuran was also found to be effective at 4.5, 9, and 13.5 g ai/cm DBH for control of C. coniperda and other associates (DeBarr et al. 1982). Permethrin at 0.3, 0.6 and 1.2 g/L applied once, and the same concentrations applied twice (14 days apart) has also provided very good control of C. ponderosae (Shea et al. 1984). At present there are no insecticides registered in Canada for control of the cone beetles.

The burning of infested cones and the use of insecticides may not always be practical. Prescribed burning, besides requiring fairly exact weather conditions, requires personnel trained in the use of fire, and to rake the cones and debris away from the base of the tree (to prevent the bark from catching fire). Soil-incorporated systemic insecticides such as carbofuran may not always be effectively translocated to the cones if the infested trees are too large or if the soil is too dry. Furthermore, concerns about ground water contamination and the environmental impact on wildlife may prohibit the use of soil-incorporated systemics in some areas. Contact insecticides such as permethrin require critical timing so that the insecticide is applied and remains effective during beetle emergence. Monitoring the emergence of caged beetles or the development of predictors such as degree-day models should be useful to determine when to spray (see Shea et al. 1984). The use of parasites, predators, pathogens, or pheromones has not been explored for the control of Conophthorus. Considerable basic research is necessary before the potential of these methods for pest management can be assessed.

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USE OF SEMIOCHEMICALS FOR MANAGEMENT OF INSECT PESTS OF CONIFEROUS SEED ORCHARDS

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ABSTRACT

The status of pheromones and kairomones for management of insect pests in coniferous seed orchards is reviewed. Sex pheromone-baited traps are used operationally to detect the presence of lepidopteran pest species, track their population trends, and determine when they are reaching damaging levels. Traps are also used to time application of insecticidal sprays. Important factors affecting the effectiveness of monitoring traps for seed and cone insects include lure dosage, trap location on host trees, and trap design. Volatile monoterpenes from pine cones that affect oviposition behavior of a coneworm pest have been identified. These kairomones may provide a useful tool for monitoring the oviposition activity of gravid females, providing a more accurate warning of potential cone damage.

RÉSUMÉ

Le présent article examine le rôle des phéromones et des kairomones dans la lutte contre les ravageurs des vergers à graines de conifères. Des pièges à phéromones sexuelles sont employés à grande échelle pour détecter la présence d'espèces de lépidoptères nuisibles, suivre leurs tendances démographiques et déterminer à quel moment elles atteignent des niveaux dangereux. Des pièges sont aussi utilisés pour déterminer le meilleur moment pour pulvériser des insecticides. Parmi les facteurs qui contribuent le plus à l'efficacité de ces pièges de surveillance des ravageurs des cônes et des graines, on note la dose d'attractif, la position du piège sur l'arbre hôte et la conception du piège. On a découvert que les monoterpènes volatils des cônes de pins affectent le comportement d'une espèce de pyrale des cônes au moment de la ponte; ces kairomones, en contribuant à révéler l'activité des femelles gravides à ce moment, peuvent fournir un signe avant-coureur plus précis de danger pour les cônes.

INTRODUCTION

Insects are a major factor limiting coniferous seed production, causing at times close to 100% seed loss (Mattson 1978, Cameron 1981, Miller 1986). Insecticides are the only practical agent available for their control but they are not always effective or acceptable, and there are few practical sampling methods for seed and cone insects to assist pest management decisions (Miller 1986). Semiochemicals, in particular sex pheromones, are now widely used for monitoring and controlling various forest insect pests (Daterman et al. 1982, Niwa et al. 1988, Grant 1989, Jutsum and Gordon 1989, Grant 1990) and their use in seed orchards is increasing to address the above problems.

The majority of semiochemicals that have practical value are either pheromones or kairomones. Pheromones mediate the behavioral interactions between members of the same species whereas kairomones are responsible for interactions between species. Figure 1 summarizes the potential semiochemical interactions that can occur in a seed orchard, involving the host trees, the seed and cone pests, and their insectan parasitoides and predators. The scheme is partly hypothetical because semiochemical data for cone and seed pests are relatively scant. Published reports deal only with sex pheromones and host-tree kairomones affecting oviposition; information on the semiochemicals affecting predators and parasitoides that attack seed and cone insects is lacking.

I. PHEROMONES AND RELATED ATTRACTANTS

Pheromones and related attractants have been identified for less than a third of the approximately 80 species of cone and seed insect pests in the USA and Canada (see Hedlin et al. 1980), and they involve only moth species (Table 1). Pheromones of important dipteran, coleopteran and hymenopteran pests have not been reported although a sex pheromone has been demonstrated for a cone gall midge (Miller and Borden 1981), and work is progressing in Canada and the USA on pheromone identifications for several Conophthorus beetle species (deGroot 1989, pers. commun.).

Pheromones can be used to manage insect pests in two ways: indirectly, as lures in traps to detect or monitor their populations, and directly by mating disruption or mass trapping to prevent their reproduction.

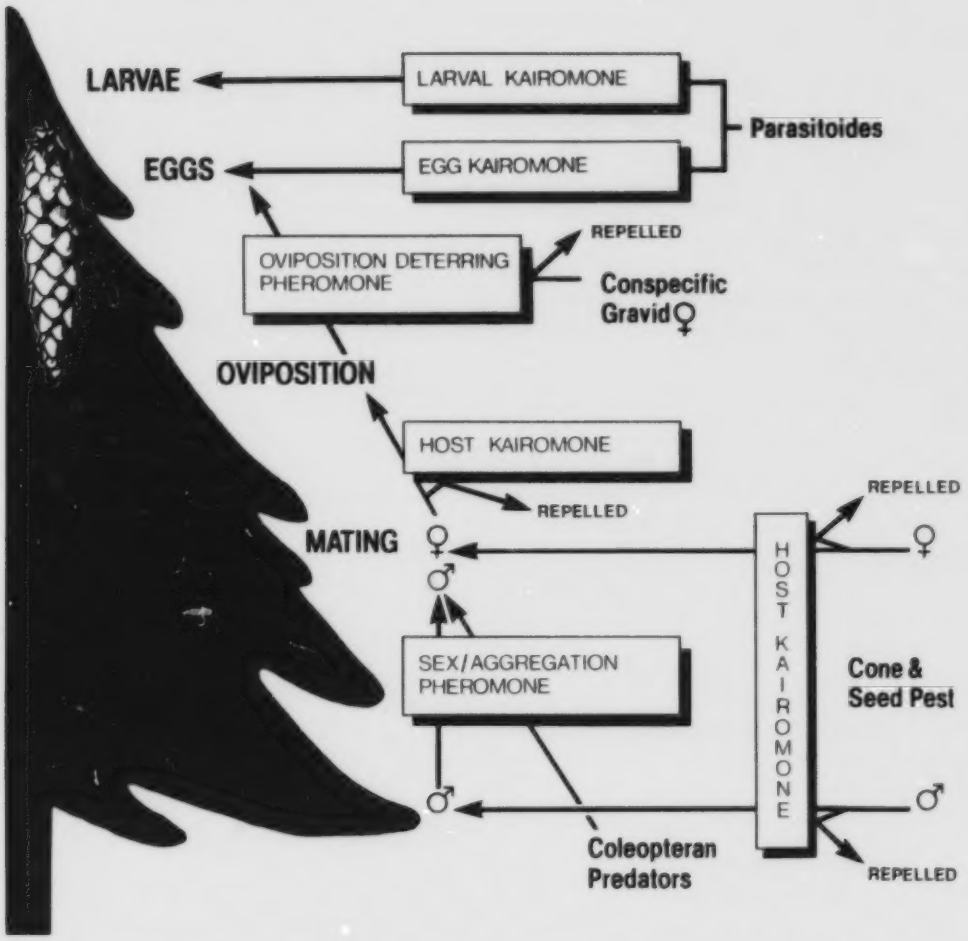

Fig. 1. The "semiochemical seed orchard": The behavior of cone and seed insects (which includes host location, female calling behavior, and male perception of pheromone) may be influenced by host volatiles. Once on or near the host, mating is controlled for many species by sex pheromones. Coleopteran species, however, usually rely on aggregation pheromones which attract both sexes, promoting colonization of the host and mating. Selection of oviposition sites by gravid females may depend on volatiles from the flowers or cones or other sources, and females of some species may deposit a pheromone as they lay their eggs which deters conspecific females from ovipositing on the same site. Insectan predators and parasitoides often utilize chemical cues from their insect hosts to find them or to stimulate oviposition behavior. Although not shown, some predators and parasitoides may locate their insect prey by using kairomones from the host trees used by the prey. Any of these semiochemical interactions, where they exist, are potentially susceptible to exploitation or manipulative intervention to control conophagous insect pests.

Table 1. Reported sex pheromones and sex attractants for insects affecting coniferous cone and seed production in North America.

Species	Attractive Compounds	Effective Ratio	Status[1]	References
Barbara colfaxiana (Douglas-fir cone moth)	Z9-12:OH Z9-12:Ac	75:25	A	Hedlin et al. 1983
Barbara mappana	E9-12:Ac		A	Reed et al. 1985
Choristoneura fumiferana (spruce budworm)	E11-14-Ald Z11-14-Ald	95:5	P	Silk et al. 1980 (and refs. therein)
Choristoneura lambertiana subretiniana	E11-14:Ac Z11-14:Ac E11-14:OH Z11-14:OH	9:6:1:0.6	P	Daterman et al. (in Harvey 1985)
Choristoneura occidentalis (western spruce budworm)	E11-14:Ald Z11-14:Ald	90:10	P	Silk et al. 1982
Choristoneura pinus pinus (jack pine budworm)	E11-14:Ac Z11-14:Ac E11-14:OH Z11-14:OH	23:4:3:0.4	P	Silk et al. 1985
Cydia colorana (pinyon seedworm)	E8,E10-12:Ac		A	Stevens et al. 1985
Cydia ingens (longleaf pine seedworm)	E8,E10-12:Ac		P	DeBarr et al. 1984
Cydia piperana (biotype)	E9-12:Ac Z9-12:Ac	1:1 7:3	A	Stevens et al. 1985 Sartwell et al. 1985
Cydia strobilella (spruce seed moth)	E8-12:Ac		A	Grant et al. 1989 (and refs. therein)
Cydia toreuta (eastern pine seedworm)	E8,Z10-12:Ac		P	Katovich et al. 1989

.../Cont'd.

Table 1. (Concl'd.)

Species	Attractive Compounds	Effective Ratio	Status	References
Dioryctria abietivorella (fir coneworm)	Z9,E11-14:Ac Z9-14:Ac		A[2]	Grant et al. (unpublished data)
Dioryctria amatella (southern pine coneworm)	Z11-16:Ac		A	Meyer et al. 1984
Dioryctria clarioralis (blister coneworm)	Z9-14:Ac E9-14:Ac Z11-16:Ac	100:12:5-10	P	Meyer et al. 1984
Dioryctria disclusa (webbing coneworm)	Z9-14:Ac		P	Meyer et al. 1982
Dioryctria ebeli	Z9,E11-14:Ac		A[2]	DeBarr et al. 1984
Dioryctria merkeli	Z9-14:Ac E9-14:Ac	100:15	A	Meyer et al. 1984
Dioryctria reniculelloides (spruce coneworm)	Z9-14:Ac Z7-12:Ac	3:0.5-0.3	P	Grant et al. 1987
Eucosma bobana (pinyon cone borer)	Z9-12:Ac		A	Stevens et al. 1985
Eucosma ponderosae (western pine cone borer)	Z9-12:Ac		A	Stevens et al. 1985
Eucosma recissoriana (lodgepole pine cone borer)	Z9-12:Ac E9-12:Ac	80:20 50:50	A	Shea et al. 1986 Stevens et al. 1985
Rhyacionia buoliana (European pine shoot moth)	E9-12:Ac Z9-12:OH	97:3	P	Smith et al. 1974 Gray et al. 1984
Rhyacionia frustrana (Nantucket pine tip moth)	E9-12:Ac E9,11-12Ac)	95:5	P	Hill et al. 1981

[1]P = sex pheromone, A = sex attractant

[2]Based on laboratory bioassays.

Detection, Survey and Monitoring Traps

In order to make rational pest control decisions, orchard managers use various sampling programs to detect insect pests and estimate their present or future impact (Miller 1986). Current methods for sampling larvae or eggs are often tedious, time-consuming and costly, and the process is destructive when the cones are cut open. Light traps provide information on both male and female adults (Yates and Ebel 1975), but the lack of species specificity and the requirement for electrical power are significant handicaps.

Pheromone traps, on the other hand, are easy to use, economical and extremely versatile. Their specificity and sensitivity are ideal for detecting the presence of pest species in seed orchards, particularly at low densities, and for determining the initiation, duration and amplitude of their flight periods (DeBarr et al. 1982, 1984; Weatherby et al. 1985; Shea et al. 1986). Knowing when and where a pest flies can be used, sometimes in conjunction with a degree-day model, to time the application of an insecticidal spray to kill adults or newly emerged larvae before they enter cones (Gargiullo et al. 1983; Haverty et al. 1986). Trap catch data can also be used to index the relative population density, predict potential damage, and thus determine the necessity for control operations (Weatherby et al. 1985).

Two pheromone monitoring programs are operational in coniferous seed orchards. Across the southeastern United States, pheromone traps track local and regional population trends of four sympatric species of Dioryctria coneworms, identifying which species are likely to be a problem in particular orchards (DeBarr et al. 1982, 1984; Weatherby et al. 1985). As in several other pheromone monitoring systems used in forestry (Grant 1990), trap catch thresholds have been adopted to translate catches into hazard ratings for coneworm damage. An average catch of <10 coneworm moths per trap, for example, indicates a low probability of damage, whereas >50 moths per trap indicates a high risk of damage and that some control action is probably needed (Weatherby et al. 1985). In Idaho, a pheromone monitoring system is used operationally in western white pine, Pinus monticola, seed orchards to detect the presence of the lodgepole pine cone moth, Eucosma recissoriana (Shea et al. 1986, Daterman 1989, pers. commun.). Because of the high value of the clones in these orchards, there is little tolerance for insect damage, so any moth capture usually triggers the application of an insecticide. In eastern Canada, pheromone traps are being deployed experimentally as a survey tool in seed production areas to detect the presence of Dioryctria coneworms and the spruce seed moth, Cydia strobilella.

Many factors contribute to an effective pheromone monitoring system (Grant 1989). Lure potency is critical and the optimum dosage for traps varies considerably from species to species (Table 2). Those for the spruce coneworm, D. reniculelloides, and

Table 2. Optimum lure dosages for selected conophagous pests.

Species	Main Component	Optimum Dosage (μg)	Ref.
Dioryctria amatella	Z11-16:Ac	100 - 300	Meyer et al. 1986
D. disclusa	Z9-14:Ac	30 - 300	Meyer et al. 1984
D. clarioralis	Z9-14:Ac	30	Meyer et al. 1982
D. reniculelloides	Z9-14:Ac	3	Grant et al. 1987
Cydia strobilella	E8-12:Ac	0.3 - 3	Grant et al. 1989

the spruce seed moth are unusually low and knowledge of this was essential in demonstrating the effectiveness of their respective attractants (Grant et al. 1987, Grant et al. 1989). Trap location on the host tree is another important factor. For Dioryctria species, greatest trap catch occurs near the tops of trees with traps in the tallest trees being the most effective (Hanula et al. 1984, Grant et al. 1987). Similarly for the the spruce seed moth (Grant et al. 1989), and the related acorn-infesting C. latiferreana (Peacock et al. 1988), greatest trap catch occurs near the tops of trees even though these moths emerge at ground level.

The effect of trap design has not been extensively explored for seed and cone insects, but its importance for trapping southern coneworm species has been demonstrated (Hanula et al. 1984). Of four trap designs evaluated, only white Pherocon IC traps were effective for these moths. However, when used for the spruce coneworm, these traps readily filled with spruce budworm, Choristoneura fumiferana, moths, which fly at the same time and blunder into the traps (Grant et al. 1987). The problem was corrected by using Pherocon ICP traps which have a much smaller opening for moth entry than the IC traps.

Although sticky traps are often used for monitoring, they have a tendency to saturate at moderate population levels, which means that they must be serviced frequently to remove captured insects. Large capacity, so-called nonsaturating traps, such as Multi-pher traps (Jobin 1985), avoid this problem. They are being evaluated for the spruce coneworm in Ontario (Prévost and Grant, unpublished) because we foresee their use during periods when manpower may not be available to service them. Although catches have been low to date, the Multi-pher traps appear to be as effective as the Pherocon ICP traps. A potential problem with

nonsaturating traps, however, is a reduction in trapping efficiency over time caused in part by decomposition of the captured insects which become repellent (Sanders 1986, Elkington 1987). This could make calibration of catches in these traps against population density extremely difficult.

A disadvantage of sex pheromone-baited traps is that they reveal the activity of only one sex, the males. Since control measures are based on the activities of females, it is important to know whether male catch also reflects female activity. This was found to be the case for the spruce seed moth in stands of white spruce, Picea glauca, near Petawawa, Ont., where daily catches of males coincided with the emergence of male and female moths from cones maintained in outdoor cages (Fogal and Grant, unpublished data). Moth flight was also closely related to the flowering phenology of the host trees. Peak emergence of males and females in cages and peak catch of males in traps coincided with the half-pendant phase of the developing cones (Fogal and Grant, unpublished data). Thus, for timing purposes, the phenology of female flowers would be as useful as pheromone traps to indicate when moth flight is at or near its peak although traps would still be useful for determining the start of moth flight.

Another problem is that the spruce seed moth, like many other obligate cone and seed pests, can enter an extended diapause, which is not predictable. Although cone sampling provides an estimate of population density, it does not indicate whether larvae will diapause or emerge as adults. This can be determined by quantifying the intensity of the subsequent moth flight with pheromone traps.

Mating Disruption and Mass Trapping

Direct control of insect populations by mating disruption is achieved by dispersing synthetic sex pheromone into the atmosphere so that males cannot locate females and mate. In contrast to the use of insecticides, this technique requires considerably more biological information about the target pest to achieve success. It is best suited to low or moderate population levels, which fortunately is characteristic of many seed orchard pests (DeBarr et al. 1984). The high value of seed crops, the relatively small areas involved in seed orchards, and the easy access to them also favor the application of mating disruption.

Preliminary mating disruption trials have been conducted in loblolly seed orchards (Debarr et al. 1984, DeBarr, pers. commun.). A test involving D. disclusa in which its pheromone, (Z)-9-tetradecenyl acetate, was released from Conrel fibers apparently failed because the initial population was too high and the pheromone levels released were too low. Two additional tests involving D. amatella in which its pheromone, (Z)-11-hexadecenyl acetate, was released from Conrel fibers or PVC pellets were inconclusive because the initial populations were too low to detect disruption effects. Subsequent tests with Dioryctria

species, however, have managed to shut down catches in monitoring traps baited with synthetic pheromone or live females (DeBarr 1989, pers. commun.). Reduction in cone damage or seed loss, the benchmark of a successful control operation, has not yet been achieved. However, mating disruption has been successful in reducing damage in pine plantations caused by Rhyacionia tip moths (Niwa et al. 1988) and Eucosma shoot borers (Daterman et al. 1982). Because pine plantations and their insect pests can be considered surrogates for coniferous seed orchards and their pests, these successes indicate that the prospects for protecting seed orchards by mating disruption are excellent. Factors that will promote success are low to moderate insect levels, isolated orchards to prevent immigration by gravid females, and effective methods of efficacy assessment.

There are no published mass trapping trials involving cone and seed insects but some success has been obtained in suppressing bark beetles and lepidopteran pests in deciduous fruit orchards with this technique (Roelofs 1979). These trials are instructive because fruit orchards are similar in nature to coniferous seed orchards. In general, success with this technique has occurred with low initial insect populations and isolation of the orchards from sources of reinfestation. In view of its similar requirements it is not clear what circumstances would favor the use of mass trapping over mating disruption in seed orchards, but mass trapping could be used as a mopping up operation, supplementing other methods of control that are less effective at low population levels.

II. HOST FINDING, OVIPOSITION, AND DETERRING SEMIOCHEMICALS

Attraction of phytophagous insects to oviposition sites, and oviposition itself, are often linked to the presence of specific chemical cues (kairomones) emitted by the host plant (Figure 1). Volatile monoterpenes of conifers, for example, attract or repel ovipositing lepidopteran females (Leather 1987). In addition, ovipositing females may deposit an oviposition-deterring pheromone that repels conspecific gravid females (Prokopy et al. 1984).

Little work has been reported on the oviposition behavior of dipteran and coleopteran pests of seeds and cones (deGroot 1986a,b), but there has been progress with lepidopteran pests. Preliminary electroantennogram (EAG) assays on the spruce seed moth with associated volatile monoterpenes from female flowers and twigs of Norway spruce, Picea abies, demonstrated that female antennae respond preferentially to constituents of female flowers (Ahman et al. 1988), which are distinct from those of male flowers or twigs (Borg-Karlson et al. 1985). EAG tests conducted on D. ebelli (formerly abietella) with volatiles from cones of slash pine, Pinus elliottii, demonstrated the presence of olfactory stimuli in those structures (Asher 1970). Volatile monoterpenes that stimulate oviposition by gravid females of the southern pine coneworm, D. amatella, have been identified from cones of loblolly

pine, P. taeda, (Hanula et al. 1985) and other host sources (Fatzinger and Merkle 1985). The critical monoterpenes were alpha-pinene, myrcene and limonene, and the amount and ratio of these compounds were important for eliciting optimum oviposition by this species (Hanula et al. 1985).

Oviposition-deterring pheromones and kairomones have not been reported for any cone and seed insects but they are well known for other dipteran, coleopteran, and lepidopteran pests (Prokopy et al. 1984). Among seed and cone pests, oviposition-deterring pheromones are likely to be found in the anthomyiid flies, since these pheromones have been demonstrated in other anthomyiid species (Zimmerman 1982). Oviposition-deterring pheromones or kairomones may exist for Conophthorus cone beetles since females of the red pine cone beetle, C. resinosae, do not oviposit in cones previously attacked by other cone beetles, conspecific or otherwise (Mattson et al. 1984). However, other factors may also explain this behavior.

The chemical identification of attractive and repellent ovipositional cues for cone pests offers new possibilities for protecting cone crops. The ovipositional stimulants discovered for the southern pine coneworm, for example, could be used as baits in artificial oviposition sites to monitor oviposition activity within an orchard (Hanula et al. 1985). These compounds also act as long range attractants which suggests that they could be used to monitor the flight of migrating females, providing early warning of unexpected crop damage (Hanula et al. 1985), and complementing the information on male flight provided by sex pheromone traps. Finally, the application of an oviposition-deterring pheromone has been shown to protect a fruit crop from a dipteran pest (Katsoyannos and Boller 1980). This method of crop protection could be applied to cone crops if a suitable oviposition-deterring pheromone or repellent kairomone can be found. However, developing effective measures of controlling seed and cone pests along the above lines requires a better understanding of their ovipositional behavior and the chemical stimuli which promote it.

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SAMPLING SEED AND CONE INSECTS IN SPRUCE

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ABSTRACT

Potential methods for sampling and predicting damage of seed and cone insects in spruce are reviewed and a method of egg sampling for estimating densities of the spruce cone maggot, Strobilomyia neanthracina (Czerny), and the spruce seed moth, Cydia strobilella L., is presented. The spatial distribution of eggs of both species were determined by dissecting 7866 conelets collected from four aspects of 80 trees in three sites in one or two years (four site-years). Percentage seed loss per cone was determined by collecting and dissecting mature cones from each tree. The number of eggs per conelet ranged from 0-12 for the seed moth and from 0-6 for the cone maggot. There were significant differences in egg densities of both species among crown aspects, but the trends were not consistent among site-years. The optimal number of conelets to sample per tree was two for both species. The number of sample trees required to estimate egg densities with 90% confidence and 10% error was determined for each site-year but was considered too large to be practical.

RÉSUMÉ

Cet article expose diverses méthodes pour échantilloner les ravageurs des graines et des cônes de l'épinette et pour prévoir les dommages qu'ils sont susceptibles de causer, ainsi qu'une méthode d'échantillonnage des oeufs qui permet d'évaluer les densités de mouches granivores de l'épinette, Strobilomyia neanthracina (Czerny), et de tordeuses des graines de l'épinette, Cydia strobilella L. On a déterminé la distribution spaciale des oeufs de chaque espèce en disséquant 7 866 cônelets prélevés aux quatre points cardinaux de 80 arbres dans trois stations durant une ou deux années (quatre années-stations). On a déterminé la proportion de graines perdues par cône en disséquant des cônes murs prélevés sur chaque arbre. Dans chaque cônelot, le nombre d'oeufs variait de o à 12 pour la tordeuse des graines et de 0 à 6 pour la mouche granivore. On a observé pour chaque espèce des différences significatives de densité des oeufs selon leur orientation dans le houppier, mais ces tendances n'etaient pas régulières pour chacune des années-stations. On a fixé à deux le nombre optimal de cônelets à prélever sur chaque arbre pour les deux espèces. le nombre d'arbres nécessaire pour déterminer la densité des oeufs avec un intervalle de confiance de 90% a été évalué pour chaque année-station, mais s'est révélé trop élevé pour être applicable dans la pratique.

INTRODUCTION

A substantial investment has been made in Canada in seed orchards for genetically improved stock of black, white, and red spruce (Pollard 1982). Several insects feed on spruce seeds and cones in North America but two of the more common seed destroyers are the spruce seed moth, Cydia strobilella L., and the spruce cone maggot, Strobilomyia neanthracina (Czerny), (Cameron and Jenkins 1988; Hedlin et. al. 1980; Ruth et al. 1982). The seed moth and the cone maggot have caused seed losses ranging from 1-34% and 7-60% respectively (Hedlin 1973; Schmid et al. 1981; Tripp and Hedlin 1956). Such losses can be expected to become more common as more seed orchards come into production.

When deciding whether or not controls are needed, seed orchard managers need simple methods of sampling insects and predicting seed loss. A good example is the sequential sampling method currently used to predict damage from the Douglas-fir cone gall midge in British Columbia seed orchards (Miller 1986). For spruce seed orchards, Ruth et al. (1982) suggest sampling 10 conelets per tree from 5% to 10% of the cone-bearing trees in an orchard just after pollination; if a mean of 2 conelets per tree contain eggs of either the seed moth or the cone maggot, seed losses of 10-20% may be expected. However, this method was intended as a rough guide and its errors are unknown. There are currently no verified methods for predicting seed losses with known accuracy and precision in spruce seed orchards.

We review some of the possible ways of monitoring spruce cone insects and present preliminary results of a study on the use of egg sampling to predict seed losses by the seed moth and the cone maggot.

POTENTIAL SAMPLING METHODS

Adult Sampling - Adult monitoring, either with pheromone traps or colored-sticky traps, should provide more lead time for control decisions and be less labor-intensive than methods involving collection and dissection of conelets. It may be the most practical method for an insect like the spruce seed chalcid, Megastigmus atedius Walker, that is difficult to detect in the egg or young larval stages. Adult sampling has been used to determine the need and timing of control activities for several agricultural pests, such as the codling moth, Cydia pomonella L. (Madsen and Vakenti 1973; Vakenti and Madsen 1976) and the onion maggot, Delia antiqua (Meighen) (Liu et al. 1982).

Sex-pheromones and attractants have been identified for several insects that attack spruce cones (Booij et al. 1986). These include the spruce budworms, Choristoneura fumiferana (Clem.) and C. occidentalis Free. (Weatherston et al. 1971; Silk et al. 1982), the spruce coneworm, Dioryctria reniculelloides

Mutuura & Munroe, (Grant et al. 1987), and the spruce seed moth (Grant et al. 1989). However, before their usefulness in predicting seed loss is known, trapping must be done in several sites and years to test for correlations between trap catch and seed loss.

A disadvantage of sex-pheromone traps is that they usually catch only males so trap catch may or may not reflect the location or density of egg-laying females. The densities of egg-laying females could possibly be estimated more directly with colored-sticky traps. These are currently used to monitor a variety of Dipteran agricultural pests including the apple maggot, Rhagoletis pomonella (Walsh)(Neilson et al. 1976), and the cherry fruit fly, Rhagoletis cerasi L. (Russ et al. 1973). More recently, certain colors have proven attractive to the larch cone flies, Strobilomyia melania (Ackland)(Roques 1986), S. viaria (Huckett), and S. laricis Michelsen (J. Turgeon personal communication), and the Douglas-fir seed chalcid, Megastigmus spermotrophus Wachtl. (Niwa 1988). A number of colors have recently been tested for attraction of the spruce cone maggot in white and black spruce orchards and plantations but the results, so far, are inconclusive (J. Turgeon, J. Sweeney and D. Summers, unpublished results).

The drawback of colored-sticky traps is their lack of specificity. Our experience with trapping for the spruce cone fly has shown us that certain colors catch many species of flies that, superficially, look similar to the cone fly. This results in a tedious process of clearing the insects in KOH and examining their genitalia before making a positive identification. Unless adults can be easily identified and counted on the traps, it may be easier to collect and dissect conelets in order to count cone fly eggs.

It may be possible to reduce the ratio of non-target species caught on colored-sticky traps by baiting the traps with host attractants, as has been done for the cabbage root fly, Delia radicum (L.)(Tuttle at al. 1988). Ahman et al. (1988) noted that antennal responses of spruce seed moths to flower volatiles were significantly higher in females than in males. The role of flower or cone volatiles in host searching by spruce cone insects has not been explored in detail.

Light traps have been used to monitor the levels of night-flying and crepuscular moths such as adult coneworms, Dioryctria spp., and seed moths, Cydia spp., in pine seed orchards in the southern United States (Yates and Ebel 1975). Like color-traps, they catch female moths as well as males but they are not species-specific. Separating, identifying, and counting pest species can be a tedious and time-consuming process.

Sampling overwintering populations

Johnson (1962) correlated seed loss in Douglas-fir with the number of overwintering cone gall midge larvae in the litter and

the size of the current flower crop, but the technique was based on only one year of data and was not further developed. Over-wintering larvae of the spruce budworm are commonly sampled and used to estimate defoliation levels (Dorais and Kettela 1982). A joint study (New Brunswick Department of Natural Resources & Forestry Canada-Maritimes Region) is currently underway to relate the numbers of overwintering budworm larvae to levels of seed damage in black spruce (Lester Hartling and Ron Smith, personal communication).

The spruce cone maggot has been sampled by collecting duff samples beneath cone-bearing trees after the larvae emerged in late summer but the numbers were highly variable (Fogal 1986). It may be difficult to distinguish cone maggot puparia from those of other Diptera but Roques (personal communication) is currently working on identification keys for Strobilomyia puparia. If puparia were collected and then overwintered at the seed orchard, the emerging cone maggot flies could be identified and counted. Some lead time would be lost but this technique would account for year-to-year variation in prolonged diapause and the resulting proportion of emerging adults. A drawback to this method is that it would measure only the resident population and would not take into account the number of cone flies that invade the seed orchard from the surrounding area.

Egg sampling

Counting eggs on flowers or conelets may be more tedious than checking pheromone traps but it gets around the problems of prolonged diapause and resident versus invading populations. Also, because the egg immediately precedes the damaging larval stage, errors in the amount of predicted seed loss due to variation in survivorship should be lower with egg sampling than with sampling adult or overwintering populations. Sequential egg sampling plans have been developed for the Douglas-fir cone gall midge (Miller 1986) and the Douglas-fir cone moth, Barbara colfaxiana (Kearfott), (Sweeney and Miller 1989) but have been used operationally only with the gall midge so far.

The drawback with egg sampling for the cone maggot or the seed moth is a relatively short window in which to determine egg densities and apply control measures if necessary. The incubation periods for eggs of the cone maggot and seed moth are about 5 and 10 days respectively (Tripp 1954a, b). Also, the oviposition period may shift relative to cone phenology in different years or sites (Tripp 1954b) so the time of conelet collection may affect the estimated egg densities. Oviposition should be complete when the conelets are half pendant to fully pendant but by this time some damage will have already occurred. Studies of the insects' phenology, e.g., degree-day models, should be carried out to determine optimal sampling times.

SAMPLING FOR EGGS OF THE CONE MAGGOT AND THE SEED MOTH

We present some preliminary results of a study on the distribution and sampling of eggs and small larvae of the cone maggot and the seed moth in white and Engelmann spruce in British Columbia. The objectives of this study were 1) to determine the spatial distribution of eggs of both species; 2) to determine the sample sizes required to estimate egg density with 90% confidence and 10% error; and 3) to determine the relationships between egg density and seed damage.

Methods

We collected a total of 7866 conelets from the upper crowns of 80 trees located in two natural stands and one progeny test in the interior of British Columbia. Fifteen Engelmann spruce trees were sampled at both the Bolean Lake and Coqhihalla Lakes sites in 1988 and 25 trees were sampled in a mixed progeny test of Engelmann and white spruce near Prince George in both 1987 and 1988. Conelets were collected when they were half to fully pendant and when the cone scales were closed. Two branches from each of four aspects (N,S,E,W) were selected from each tree and all conelets were collected and stored at -10°C until dissected. Each conelet was dissected scale by scale under a stereoscope (6X) and eggs and small larvae of both species were counted. Mature cones (8-16 per tree) were collected in late summer and were dissected to determine the number of seeds damaged by each insect. Seeds damaged by the seed moth are packed with frass and are easily distinguished from those fed upon by the cone maggot (Ruth et al. 1982).

Analysis of covariance and the Newman-Keul's test ($\alpha = 0.05$) were used to test for the effects of trees, aspect, and the number of conelets per branch (covariate) on the mean number of eggs per conelet per branch in each site year. Components of variance for among-tree and within-tree variation in the number of eggs per conelet were determined for each site-year using ANOVA, and were used to estimate the optimum number of conelets per tree to sample using the cost-variance formula (Southwood 1966, p. 18). The cost of selecting and moving to a sample tree was estimated to be 3 min. and the cost of collecting and dissecting a conelet was estimated to be 4 min. The number of trees per site required to estimate egg densities with 90% confidence and 10% error was determined using a formula for two-stage sampling (Southwood 1966, p. 20). The relationships between the percentage of damaged seeds per cone and: 1) the number of eggs per conelet, and 2) the percentage of infested conelets, were tested for each insect using regression analysis of the means for each tree. The regressions were forced through the origin when the intercept was not significantly different than zero (t-test, $P \leq 0.05$). Corrected sums of squares were used for calculating r^2 values (Kvålseth 1985) and for testing the significance of the regression.

RESULTS AND DISCUSSION

The number of eggs per conelet ranged from 0-12 for the seed moth and from 0-6 for the cone maggot. There were significant differences in egg density among trees for both insect species in each site-year. The number of seed moth eggs per conelet per branch varied significantly with the mean number of conelets per branch in one site-year but cone maggot egg density was not related to conelet density in any site-year. The number of eggs per conelet was significantly different between different crown aspects for the seed moth in one site-year and for the cone maggot in three site-years. However, because the ranking of aspects was inconsistent among different site-years, we concluded that conelets could be sampled randomly from the upper crown.

There were very few trees with conelets in the mid or lower crown in the four site-years sampled. Further work is needed to measure the variation in egg densities among crown levels.

Variance in the number of eggs per conelet was greater among conelets within trees (61-86%) than among trees (14-34%) for both the cone maggot and the seed moth. The optimum number of cones to sample per tree, calculated for each site-year, ranged from 1.3-2.2 for the seed moth and from 1.1-2.0 for the cone maggot. We chose two conelets per tree as an optimum sample for both species.

The number of sample trees required to estimate the egg density with 90% confidence and 10% error ranged from 223-509 for the seed moth and from 218-542 for the cone maggot. Using the costs for collecting and dissecting conelets that we estimated, it would take about 5 person-days to complete a sample of 200 trees and over 12 person-days for a sample of 500 trees. Depending on the number of cone-bearing trees in the orchard, these sample sizes could be reduced by the finite population correction (Cochran 1977) but they would remain fairly large.

Data for seed damage are complete only for 21 trees (Prince George, 1988) so far, but the regressions of percentage damaged seeds per cone versus the mean number of eggs per conelet were significant ($P \leq 0.05$) for both the seed moth ($r^2 = 0.27$) and the cone maggot ($r^2 = 0.33$)(Figs. 1A,B). Based on a maximum acceptable seed loss of 10%, the control threshold number of eggs per conelet is about 0.8 for the seed moth and 0.3 for the cone maggot. Also significant ($P \leq 0.01$), were the regressions between percentage damaged seeds per cone and the percentage of infested cones per tree; $r^2 = 0.33$ and 0.37 for seed moth and the cone maggot respectively (Figs. 2A,B). These relationships will doubtless be modified when the data from other site-years are included.

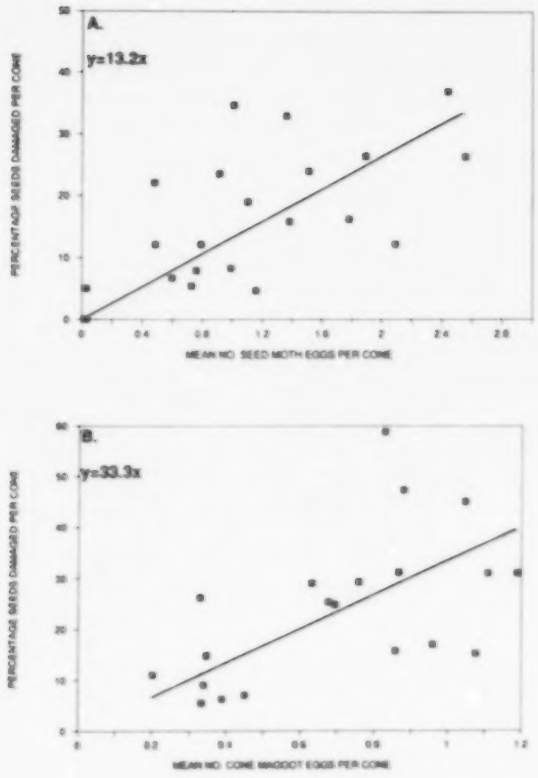

Fig. 1. The mean percentage of seeds damaged per mature cone versus the mean number of eggs per conelet for each of 21 trees; A) Spruce seed moth, and B) Spruce cone maggot. Regressions were forced through the origin and were both significant ($P < 0.05$).

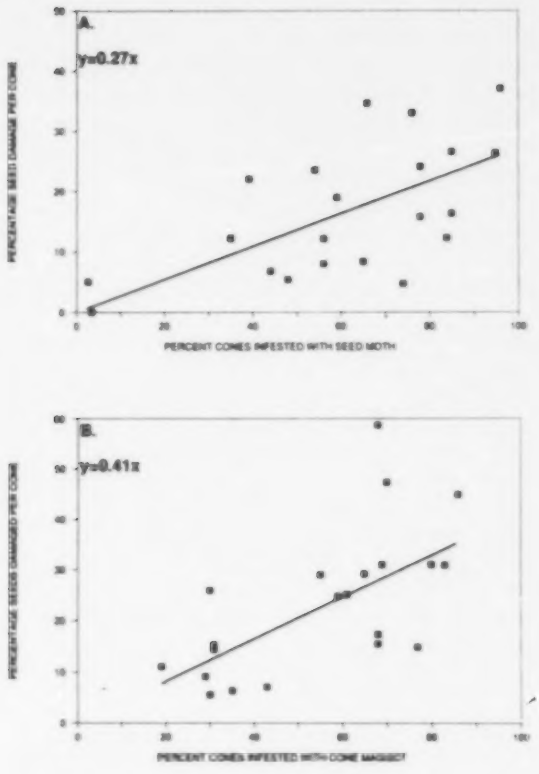

Fig. 2. The mean percentage of seeds damaged per mature cone versus the percentage of conelets infested per tree for each of 21 trees; **A)** Spruce seed moth, and **B)** Spruce cone maggot. Regressions were forced through the origin and were both significant ($P < 0.01$).

CONCLUSIONS

There are currently no statistically derived and operationally tested sampling methods for predicting seed damage with known accuracy and precision in spruce seed orchards. However, with further research efforts, several methods of monitoring may be possible, including, for example, pheromone traps for the seed moth and spruce coneworm, and colored-sticky traps for the cone maggot fly and seed chalcid. Preliminary results of an egg sampling study suggest that the percentage of seeds damaged by the spruce seed moth or the spruce cone maggot can be predicted by the mean number of eggs per conelet or the mean percentage of conelets infested with each species. However, the numbers of sample trees and conelets required to estimate lower egg densities of either species with 90% confidence and 10% error were very high. For pest management purposes it would be more practical to use a sequential sampling plan to classify the egg density above or below a damage threshold rather than trying to estimate absolute densities. Sequential plans are being developed by the authors and should soon be available for field testing.

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WHITE SPRUCE CONE CROPS IN RELATION TO SEED YIELDS, CONE INSECT DAMAGE, AND SEED MOTH POPULATIONS

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ABSTRACT

Cone crop size, seed counts per cone, and the proportion of cones damaged by several insects, along with adult abundance, larval mortality, and diapause of the spruce seed moth, were monitored in white spruce stands for several years. The number of sound seeds per cone was positively correlated with the size of the cone crop, whereas the proportion of cones damaged by insects was negatively correlated with the cone crop. The abundance of adult seed moths and the size of the cone crop were not correlated, whereas overwintering mortality and prolonged diapause were correlated with crop size. Summer temperatures influenced seed moth mortality and may have influenced prolonged diapause and cone crop size the following year.

RÉSUMÉ

Durant plusieurs années, dans des peuplements d'épinette blanche, on a enregistré le volume des cônes récoltés, le nombre de graines par cône et la proportion de cônes endommagés par divers insectes, de même que l'abondance d'adultes de la tordeuse des graines de l'épinette, la mortalité larvaire et la durée de leur diapause. Le nombre de graines saines par cône et le volume de cônes récolté ont été corrélés positivement, alors que la proportion de cônes endommagés par les insectes et le volume de cônes récolté l'ont négativement. On n'a pas corrélé l'abondance de la tordeuse adulte avec le volume de la récolte, alors que la mortalité hivernale et la diapause prolongée ont été corrélées avec le volume de la récolte. Les températures estivales ont contribué à la mortalité de la tordeuse et peuvent avoir influencé la durée de la diapause et le volume de cônes récolté l'année suivante.

INTRODUCTION

Seed yields and cone damage by insects are influenced by periodical fluctuations in annual crop size in conifer seed trees. In white spruce, Picea glauca (Moench) Voss, insect damage is usually high and seed yields are low in poor crop years, whereas the inverse occurs in good crop years (Werner 1964). Similar relationships occur in red pine (Pinus resinosa Ait.) (Mattson 1971) and western white pine (P. monticola Douglas) (Shea et al. 1984).

Kraft (1968) and Mattson (1971) postulated that crop size is a regulator of cone insect numbers on pines; small cone crops reduce populations of cone insects so that they damage few cones the succeeding year, whereas large crops have the opposite effect. Thus, stabilizing and increasing cone production in seed orchards or seed production areas might allow cone insect populations, unless checked, to expand to the limit of the food resource. This concern overlooks the effects of density-independent climatic factors that act to modify population density by direct mortality or by altering proportions of insects that enter prolonged diapause.

In this report, yearly fluctuations in seed yields and cone damage by several cone and seed insects relative to cone crop size are examined in white spruce stands for a period of seven years. Adult abundance, overwintering mortality, and prolonged diapause of the spruce seed moth Cydia strobilella (L.) are also examined to determine what role, if any, cone crops play in regulating populations of this insect. Finally, the effect of summer temperature on cone crop size, seed moth mortality, and prolonged diapause is considered.

Materials and Methods

1. Stands

Six relatively open stands were selected southwest of Pembroke, Ontario (45°49'N; 77°07'W; UTM 354760). In 1984, the average canopy height of the stands was 13.4 ± 0.7[1] m, and the basal area of the white spruce component of the stands was 23.4 ± 8.1[1] m^2 (88% of total), represented by an average of 634 ± 328[1] stems/ha. Cone-bearing sample trees, those larger than 10 cm diameter at breast height (DBH), represented 63% of the white spruce. Average age, height, and DBH of three typical sample trees from each of the six sites in 1983 were 42.5 ± 5.5[1] years, 14.8 ± 2.4[1] m, and 27.5 ± 2.8[1] cm, respectively.

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[1]Standard error of the mean.

2. Cone crop ratings

Cone crops were rated yearly from 1980 to 1986 in each of the six stands during the last week of June on five randomly selected white spruce trees old enough to bear cones. The cone crop on each tree was placed in one of the following cone classes (1, no cones; 2, 1-10 cones; 3, 11-100 cones; 4, 101-1000 cones; and 5, 1001 or more cones).

3. Cone insect foraging damage and seed yields

Insect damage to cones and cone seed yields were estimated on samples of 20 cones collected in late July and early August from each of five trees at each stand. The occurrence of insect damage by species was identified on each sample cone by noting external damage characteristic of external feeders and by examining median longitudinal sections under a dissecting microscope to identify damage characteristic of internal feeders (Tripp and Hedlin 1956, Fogal and Lopushanski 1989). All of the exposed seeds on the face of one section were then counted after classifying them as 1) sound seed containing a well-developed gametophyte; 2) empty seed with a well-developed seed coat and a dried up or missing gametophyte; 3) seeds destroyed by the seed moth and filled with frass; 4) seeds destroyed by the maggot, in which case the seed is completely absent except for fragments of the seed coat or wing tissue; and 5) seeds containing larvae of seed chalcids or seed midges.

4. Sex attractant monitoring of the seed moth

Seed moth abundance was monitored by trapping adult males in Pherocon 1C traps (Zoecon, Palo Alto, California) baited with a synthetic mixture[2] of 100 ug (E)-7-dodecenol plus 5 ug (Z)-7-7-dodecenol plus 5 ug (E)-7-dodecenyl acetate applied to red rubber septa (A.H. Thomas, Philadelphia, Pennsylvania). At each site, two traps were hung at head height on two randomly chosen trees separated by at least 20 m. The traps were set up prior to moth flight in early May of each year and were visited on alternate days to count and remove trapped males. This was done until moth flight ended.

5. Seed moth emergence, larval mortality, and diapause

Emergence of male and female seed moths from cones, and the fate of unemerged insects, were determined in cones collected from duff under trees in early May of each year prior to adult emergence. Random samples of cones, regardless of apparent age,

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[2]The synthetic sex attractant was provided by Dr. G.G. Grant, Forest Pest Management Institute, Forestry Canada, Sault Ste. Marie, Ont., Canada P6A 5M7.

were collected from each site and placed in screened cages (50 cm x 35 cm x 35 cm). From 1981 to 1984, 200 cones were placed in each cage; following a bumper cone crop in 1984, 1000 cones were placed in each cage. The cages were placed at one centrally located site to reduce losses resulting from vandalism and cattle disturbance. In 1981, six cages, each containing cones from one site, were set up. From 1982 to 1986, 12 cages were set up, consisting of two replicate collections from each of the six sites. Adults were collected from the cages on alternate days using a siphon trap and were sexed by examining their genitalia. At the end of emergence, all cones were dissected to count the numbers of dead or living larvae or pupae remaining in the axis gallery. Specimens were considered to be dead if they were dehydrated, brownish in color, flaccid, and did not move when probed; living specimens had turgid, ivory-colored bodies and moved when probed.

6. Weather records

Records of daily maximum, minimum, and mean temperatures and precipitation at Petawawa airport for 1980-1986 were obtained from Atmospheric Environment Service, Environment Canada, Downsview, Ontario.

7. Statistical analyses

All percentage data, including percent cone damage, insect mortality, and diapause were transformed to arcsine $\sqrt{\%}$ before being analyzed. Cone crop ratings and seed and insect counts were not transformed. Analyses of variance were carried out to test for differences among years and sites and correlation coefficients were calculated to determine associations between paired variables (Steel and Torrie 1960).

RESULTS AND DISCUSSION

1. Cone crops, seed counts, and insect foraging damage

Analyses of variance to compare sites, years, and their interactions revealed highly significant differences ($P < 0.01$) among years for cone crop ratings, and seed counts, and percent cone damage. There were significant differences among sites for cone crop ratings ($P < 0.01$) and for some of the insects ($P < 0.05$), but not for any of the seed counts. Significant interaction among sites and years ($P < 0.05$) was evident for some of the insect damage and seed count variables, and for cone crop ratings. Although cone crop ratings differed among sites, the sum of squares for years represented 88% of the model sum of squares. For those insects where differences in cone damage among sites were noted, the sums of squares for years represented the following proportions of the model sums of squares: coneworm, 56%; seed moth, 90%; cone maggot, 87%; cone-axis midge, 36%; and cone gall midge, 71%. Because differences among years represent a

larger proportion of variation in the ANOVA model for most variables compared to sites and because this study is primarily concerned with yearly fluctuations of crop and insect variables, the presentation of results and discussion deals only with differences among years.

Cone crop ratings varied from a crop failure in 1985 to a heavy crop in 1982 and a very heavy crop in 1984 (Table 1); for the remaining years, crops were low to moderate in size. The number of sound seeds per cone section was positively correlated with the size of the cone crop ($r = +0.85$; $P = 0.03$); thus, the largest number of sound seeds occurred when the crop size was above average. The number of sound seeds represented 6-41% of total seeds per cone section. Empty seeds made up 34-54% of the totals, suggesting that substantial numbers of seeds had aborted. Such losses are common in white spruce (Tripp and Hedlin 1956, Owens and Molder 1979).

Insects were responsible for substantial losses of seeds, with 2-28% of the losses being attributed to the seed moth and 10-17% being attributed to the cone maggot. Smaller losses (0-6%) were attributed to seed-inhabiting insects. Seeds destroyed by insects such as the coneworm that feed indiscriminately on all cone tissues could not be counted. Hence, total seed does not reflect the total potential seeds per cone (Table 1).

The proportion of cone damage attributed to particular insects varied substantially among species and years (Table 1). Damage by the seed moth, the cone maggot, and seed inhabitants was observed most frequently. The proportions damaged by all of the insects ranged from 41% to 100% and were negatively correlated with the size of the cone crop ($r = -0.81$; $P = 0.05$). Thus, for the period of time over which this survey was conducted, variations in the size of the cone crop can explain annual variations in the proportion of cones damaged by all insects. However, when individual species were considered, correlations of damage with cone crop size were not statistically significant. Apparently, some factor or factors other than cone crop size play a role in the annual fluctuations of the damage caused by individual species. Perhaps inter- and intraspecific competition, other mortality factors, and prolonged diapause are important.

2. Seed moth emergence, abundance, mortality, and diapause

Sex attractant traps caught the largest numbers of males in 1981; numbers then declined to their lowest levels in 1984, and remained low (Table 2). The emergence of males and females from cones followed this trend closely. Correlation coefficients of trap catch with male and female emergence were +0.94 ($P = 0.005$) and +0.87 ($P = 0.03$), respectively, indicating that trap catch reflects the intensity of moth flight from year to year. The abundance (trap catch) of adults was not significantly correlated

Table 1. White spruce cone crop ratings, seed counts, and percentage of cones damaged by insects for crop years 1980-86.

	Year						
	1980	1981	1982	1983	1984	1985[1]	1986
Cone crop rating	2.1±0.2[2]	2.8±0.2	3.9±0.1	2.6±0.1	4.2±0.1	1.1±0.1	1.6±0.1
Seeds per 10 cone sections							
Sound seeds	37±5	28±6	72±5	7±1	67±5	-	11±3
Empty seeds	-	68±6	60±5	64±4	72±5	-	46±4
Seeds damaged by seed moth	67±4	46±5	25±2	20±2	3±1	-	29±3
Cone maggot	71±1	2±1	3±1	20±2	18±1	-	15±2
Seed inhabitants[3]	7±1	2±1	3±1	7±2	1±1	-	3±0
Total seed	-	169±1	176±6	118±5	160±3	-	103±3
Percentage of cones damaged by insects							
Budworm	16±5	10±1	14±3	12±2	2±0	-	20±4
Coneworm	1±1	4±1	9±2	10±3	1±1	-	2±1
Seed moth	92±2	65±5	46±5	40±3	6±3	-	57±4
Cone maggot	94±1	35±4	24±1	31±3	31±7	-	30±6
Cone-axis midge	0±0	3±1	9±5	4±1	0±0	-	4±1
Cone gall midge	0±0	0±0	7±2	12±2	1±1	-	19±4
Seed inhabitants[3]	34±6	12±3	15±4	33±5	3±1	-	19±4
All insects	100±1	88±3	81±1	88±4	41±6	-	93±2

[1] Insufficient cones available for analysis.

[2] Standard error for six sites.

[3] Larvae of a seed chalcid or a seed midge.

Table 2. Males of Cydia strobilella in sex attractant traps, male and female emergence from cones, and live or dead larvae and pupae remaining in cones from 1981-86.

Year	Males per trap	Insects per 1000 cones in emergence cages (percentage of total in parentheses)						
		Males emerged	Females emerged	Larvae		Pupae		Total
				Live	Dead	Live	Dead	
1981	95±14[1]	23±5 (21)	24±2 (21)	27±7 (24)	29±10 (26)	9±6 (8)	0±0 (0)	113±30 (100)
1982[2]	46±22	14±4 (-)	24±7 (-)	- (-)	- (-)	- (-)	- (-)	- (-)
1983	10±4	6±4 (2)	4±2 (1)	151±20 (52)	130±21 (44)	0±0 (0)	2±1 (1)	292±48 (101)
1984	6±2	4±2 (4)	5±1 (5)	1±1 (1)	107±22 (89)	0±0 (0)	2±1 (2)	120±27 (101)
1985	14±4	0±0 (0)	0±0 (0)	5±2 (86)	1±0 (14)	0±0 (0)	0±0 (0)	6±2 (100)
1986	12±7	0±0 (4)	0±0 (4)	2±1 (60)	1±0 (20)	0±0 (7)	0±0 (5)	4±2 (100)

[1] Standard error for six sites.

[2] Cones were not analyzed for the occurrence of seed moth larvae and pupae in 1982.

($r = +0.64$; $P = 0.25$) with the proportion of cones damaged by this insect (Table 2) over the same time period; trap catch may not, therefore, provide a good prediction of eventual damage to cones. In addition, adult abundance was not related to the available food supply as the correlation coefficient for trap catch with cone crop size was not significant ($r = +0.17$; $P = 0.75$). Annila (1984), also, found that emergence of the seed moth was not consistently related to the size of the cone crop.

Most seed moths remaining in the cone-axis gallery were in the larval stage but a small number of pupae were also present. Living and dead individuals were found at each stage. The proportion of dead individuals varied positively with the size of cone crop ($r = +0.91$; $P = 0.03$). The largest proportions occurred in 1984, following a year when the crop was relatively low and large proportions of cones were damaged. The smallest proportions occurred in 1985, following a bumper crop in which small proportions of cones were damaged.

Live larvae and pupae remaining in cones after adult emergence is completed are considered to be in a state of prolonged diapause. The proportion that remained alive in diapause was negatively correlated with the size of the cone crop ($r = -0.98$; $P = 0.003$). The lowest incidence of diapause occurred in 1984 during the heavy cone crop and the highest incidence occurred in 1985, when the crop failed. Intermediate levels occurred in other years. Such a relationship between prolonged diapause of this seed moth and the size of cone crops has also been demonstrated in studies on Norway spruce (Bakke 1963).

Stadnitskii (1986) suggests that tree reproduction dynamics and cone insect diapause are influenced by similar natural factors. High temperatures during floral initiation and insect larval development are considered to predispose spruce trees to produce large numbers of flowers the following year (Fraser 1958, Lindgren et al. 1977, Owens and Molder 1979) and to prevent induction of prolonged diapause in the seed moth (Bakke 1963) and another cone insect, the Douglas-fir cone moth Barbara colfaxiana (Kearfott) (Hedlin et al. 1982). High temperatures during larval feeding may weaken the seed moth and lead to mortality in later stages as it does in other insects (Fogal and Kwain 1972). Did temperature affect the size of the cone crops, seed moth diapause, and mortality during this study? To answer this question, climatic records were examined and it was found that average maximum daily temperatures for the months of June, July, and August in 1983 were substantially higher than normal. This was the year preceding the bumper cone crop, high seed moth mortality, and low incidence of seed moth diapause. To further substantiate possible relationships with temperature, correlation coefficients were calculated for average maximum daily temperatures for the months of May through August with the size of the cone crop, seed moth mortality, and diapause in the succeeding year for the five years over which the seed moth parameters were determined. For cone crops, the correlation coefficient was +0.74 ($P = 0.06$) and

for diapause incidence it was -0.84 (P = 0.07), nearly approaching acceptable levels of significance. For mortality, the coefficient was +0.92 (P = 0.03). Temperature during the summer of larval feeding and flower initiation does, in fact, appear to have influenced larval mortality in the following year and may also have influenced diapause incidence and cone crop size. Thus, cone crop size, seed moth diapause, and seed moth mortality were coincidentally related through the action of temperature. Temperature acts directly on the tree and may act directly on the insect or indirectly on the insect through temperature-induced changes in the tree. In addition, overwintering insects that had been subjected to severe inter- and intraspecific competition while feeding in years when crops were small might have been more susceptible to abiotic and biotic mortality factors. In this way, the cone crop size might, indeed, act as a regulator, controlling the abundance of cone and seed insects as postulated by Kraft (1968) and Mattson (1971). Prolonged diapause, then, may be a mechanism whereby populations of cone and seed insects escape years of poor or nonexistent seed production and avoid inter- and intraspecific competition as postulated by Bakke (1963), Miller and Hedlin (1984), Stadnitskii (1986), and Roques (1989).

CONCLUSIONS

Data from this study show that the size of the cone crop influences seed yields, with the largest numbers occurring when crops are above average. Cone damage by all insects was negatively correlated with the size of the cone crop, but for individual species the relationship did not hold. Fluctuations in the abundance of spruce seed moth adults were not related to annual variations in the cone crop, but larval mortality was positively correlated with the size of the cone crop and prolonged diapause was negatively correlated with the size of the cone crop. Summer temperatures appeared to influence cone crops, seed moth mortality, and seed moth diapause in the succeeding year; high temperatures favoured large cone crops and high seed moth mortality, and prevented prolonged diapause. Prolonged diapause allowed some seed moth larvae to wait out years when crops were low or nonexistent at the risk of increased mortality the following year. If large cone crops improve the chances of insect survival by reducing inter- and intraspecific competition, then a buildup of insect populations might be favored if crops can be stabilized at a high level by seed orchard management techniques. However, insects will still be influenced by climatic factors, which appear to play a very important role in regulating the abundance of one of them, the spruce seed moth. This has important implications for pest management decisions in highly managed seed orchards and needs to be considered in more detail for the spruce seed moth and other insects that feed on cones and seeds of white spruce and other commercially important conifers.

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CLONAL VARIATION IN SUSCEPTIBILITY TO DAMAGE BY INSECTS INFESTING CONES AND SEEDS IN BLACK AND WHITE SPRUCE SEED ORCHARDS: PRELIMINARY RESULTS

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ABSTRACT

In 1988, genetic variations in cone susceptibility to insect attack were evaluated using cones collected from seed orchards of black spruce Picea mariana (Mill.) B.S.P., and white spruce, P. glauca (Moench) Voss located in northern Ontario. The proportions of cones damaged by Lepidoptera (e.g. Choristoneura spp., Dioryctria spp., Coleotechnites spp., etc,) and infested by the spruce cone maggot (SCM), Strobilomyia neanthracina Michelsen, were determined for both coniferous species, whereas the proportion of cones infested by the spruce seed moth (SSM), Cydia strobilella (L.), was determined for white spruce only. The seeds of these cones were extracted and irradiated with X-rays to estimate the proportion destroyed by seed-insects (e.g. Cecidomyiidae). No statistically significant differences in the percentage of cones damaged by SCM, SSM, and Lepidoptera spp. were detected among clones of black and white spruce. The number of seeds infested by Cecidomyiidae was too low to perform a statitical analysis.

RÉSUMÉ

En 1988, des cônes d'épinette noire, Picea mariana (Mill.) B.S.P., et d'épinette blanche, P. glauca (Moench) Voss, ont été récoltés dans des vergers à graines du nord de l'Ontario dans le but de mettre en évidence des variations génétiques dans le taux d'attaque par les insectes. Nous avons donc déterminé, pour les deux espèces de conifères, le pourcentage de cônes attaqués par les larves de lépidoptères (i.e. Choristoneura spp., Dioryctria spp., Coleotechnites spp., etc,) et par la mouche granivore des cônes de l'épinette, Strobilomyia neanthracina Michelsen. Nous avons également déterminé, mais seulement pour l'épinette blanche, le pourcentage de cônes attaqués par la tordeuse des graines de l'épinette, Cydia strobilella (L.). Egalement, les graines de cônes examinés ont été extraites et radiographiées afin de détecter la présence d'insectes s'attaquant uniquement aux graines (i.e. Cecidomyiidae). Les résultats, bien que préliminaires, n'indiquèrent aucune différence interclonale. Dû au nombre trop faible de graines attaquées par les Cecidomyiidae, aucune analyse statistique n'a été réalisée.

INTRODUCTION

As a result of expanding reforestation programs throughout the world, seed orchards have been established and managed to produce frequent, abundant, and easily harvested crops of genetically superior seeds. These orchards are also used to maintain genetic diversity. To ensure diversity in seed orchards, ramets are systematically placed to maximize random cross-pollination. However, the timing of pollen release and female receptivity as well as the number of male and female strobili produced by the various clones can also influence the amount and the genetic composition of seeds harvested from seed orchards (O'Reilly et al. 1982). Furthermore, insects infesting the tree's reproductive structures (pollen- and seed-cones) can significantly alter the genetic diversity of a seed orchard's progeny by concentrating their attack on specific clones. Significant clonal differences have been reported in attack by insects infesting the cones of Douglas-fir (Hedlin and Ruth 1978; Roques 1981; Schowalter and Haverty 1989), slash pine (DeBarr et al. 1972; Merkel et al. 1965), loblolly pine (Askew et al. 1985; Williams and Goyer 1980) and western white pine (Jenkins 1983).

In the past decade, several hundred hectares of black spruce, Picea mariana (Mill.) B.S.P., and white spruce, P. glauca Moench (Voss), have been established in eastern Canada. Most insect species infesting the cones and seeds of black and white spruce, in plantations and in natural stands, have already been identified (Bonneau et al. 1986; Fogal 1979; Hedlin et al. 1981; Kondo and Taylor 1984; Kondo and Moody 1987; Lachance et al. 1985; Prévost et al. 1988; Sterner and Davidson 1983). Among the most important pests are the spruce cone maggot, Strobilomyia neanthracina Michelsen (= Delia = Hylemya = Lasiomma anthracina in North American literature), which destroys the seeds of both black and white spruce and the spruce seed moth, Cydia strobilella (L.), which infest mostly white spruce cones. Also, the combined feeding of several species of Lepidoptera (defoliators, needle-miners, etc) often represent the most important source of cone mortality (Prévost et al. 1988). Although several components of the reproductive dynamics of black and white spruce have already been studied (McPherson et al. 1982; O'Reilly et al. 1982; O'Reilly 1981; Stoehr and Farmer 1986), there is, however, no information available on the influence of black and white spruce genotypes on losses to insects infesting cones and seeds.

The objective of this study was to determine if, in seed orchards, ramets of black and white spruce differ in susceptibility to S. neanthracina, C. strobilella, Lepidoptera spp. and Cecidomyiidae (Diptera).

MATERIALS & METHODS

Cones for this study were collected in 1988 from seed orchards located in northern Ontario (Table 1). Overall, the 1988 cone crop was rated as good and excellent for black and white spruce, respectively. For both species, the 1987 and 1986 crops varied between nil and poor (F.V. Haavisto, pers. comm.).

Table 1. Location of seed orchards, and number of blocks[1] and clones sampled, Ontario 1988. Sb = black spruce, Sw = white spruce.

Seed Orchard	Host	No. blocks	No. Clones
Longlac (49 47'N, 86 30'W)	Sb	Entire orchard[2]	44
	SW	Entire orchard	44
O'Connor (48°22'N, 89°42'W)	Sb	2 blocks (1973[3] A & B)	30
	Sw	2 blocks (1973 A & D)	39
Matawin (48°23'N, 90°03'W)	Sb	1 block (1966 A)	9

[1] Originally all blocks contained 12 clones represented by 12 ramets.
[2] Orchard of uneven age with planting carried out between 1958-1978.
[3] Year the block was planted.

Where possible, 5 cones were taken from each ramet at the time of seed maturity, in early September. The number of ramets from each clone varied between 1 and 14. The cones were stored in cloth bags at 4°C until processed. In January, the volume of each cone was determined by water displacement to the nearest 0.5 mL. Cones infested by S. neanthracina, as indicated by the presence of an exit hole, and those damaged by Lepidoptera spp. larvae were recorded. The proportion of seeds infested by Cecidomyiidae was determined from a random subsample of 10 cones taken from each clone. All cones were used from clones producing less than 10 cones.

Black spruce seeds were extracted by soaking cones in cold water overnight and by removing the seeds by hand after drilling through the cone axis. White spruce cones were air dried individually at room temperature (ca 21°C). Seeds remaining in these cones after 2 weeks were removed with forceps. The seeds of each cone were irradiated for 3 min at 14 Kv using a Faxitron X-ray unit (model 8040). The radiographic image of the seeds was examined with a magnifying glass (5X). The number of filled seeds

examined with a magnifying glass (5X). The number of filled seeds and seeds infested by Cecidomyiid larvae were recorded. The cones from the January subsample and those from the initial sample taken in September were then bisected to determine the proportion of cones infested by C. strobilella.

In each orchard, an analysis of variance (ANOVA) with clones and proportion of infested cones being the independant and dependant variables, respectively, was performed for each insect or group of insects (e.g. Lepidoptera spp.) using BMDP 7D (BMDP Statistical Software Manual, pp 187-209). This ANOVA was performed after the proportions of infested cones had been transformed by arcsin proportion to stabilize the variances. Only clones with cones sampled from two ramets or more were considered in the ANOVA. Because the Levene test included in the BMDP 7D revealed that the variances were significantly different ($P < 0.05$), the Brown-Forsythe procedure was used to test the equality of clone means. The inequality of variance even after transformation was undoubtedly related to the low and variable number of ramets/clone producing cones and to the low proportion of damaged cones.

RESULTS & DISCUSSION

Among the mature cones collected in September, the proportion damaged by insects was below 7% in all orchards (Table 2).

Table 2. Proportion of cones damaged by insects in 3 seed orchards, Ontario 1988.

Host Orchard	N[1]	Healthy (%)	Damaged by: Lepidop. (%)	Spruce Seed Moth (%)	Spruce Cone Maggot (%)
White Spruce					
Longlac	859 (33)	94.5	1.7	0.0	3.8[2]
O'Connor	555 (28)	95.1	4.9[2]	0.0	0.0
Black Spruce					
Longlac	1350 (41)	96.7	3.3[2]	0.0	0.0
O'Connor	300 (30)	97.7	2.3[2]	0.0	0.0
Matawin	90 (9)	93.3	6.6[2]	0.0	0.0

[1] No. of clones with 2 or more ramets, in brackets.
[2] Indicates that no statistically significant differences were detected among the clones of that orchard ($P = 0.05$).

The Lepidoptera were responsible for all of this damage except in Longlac, where they attacked 1.7% of the white spruce cones compared with 3.8% for the spruce cone maggot. None of the cones examined were infested by the spruce seed moth. The low proportion of cones infested by S. neanthracina and C. strobilella is probably due to the limited availability of cones in 1986 and 1987. This inverse relationship between the proportion of cones infested and cone abundance has been demonstrated for several insects (Mattson 1971; Stadnitzky and Smetanin 1985). The incidence of attack by these two pests is not affected by the premature drop of the infested cones.

The proportion of cones damaged by Lepidoptera spp. did not differ significantly among clones within the same orchard. Also, there is no evidence suggesting that the severity of the damage inflicted by the Lepidoptera spp. on black and white spruce cones may vary among clones, because none of the damaged cones were deformed. This observation may be due to the low population levels. To assess the impact of this light damage by Lepidoptera spp., I compared the volume and the number of filled seeds per healthy and damaged black and white spruce cones (healthy cones were selected from the same ramet as those damaged by Lepidoptera spp.). For both host species, no significant differences were detected (Table 3). Prévost et al. (1988) reported similar results for lightly damaged black spruce cones.

The proportion of cones infested by S. neanthracina did not differ significantly among any of the clones collected from the Longlac white spruce seed orchard ($F = 1.06$; $DF = 32, 31$; $P > 0.43$). Because of the low number of infested cones per clone, it was impossible to determine whether the seed-destroying capacity of S. neanthracina varied among clones. When the clonal influence is removed, the volume and the number of filled seeds of S. neanthracina-infested cones were significantly smaller than that of healthy cones (Table 4). Because of the low density estimates, I suspect that this damage, which resulted in the destruction of ca. 75% of the filled seeds, was caused on average by a single larva of S. neanthracina. Tripp and Hedlin (1956) reported that, on average, one spruce cone maggot destroyed ca. 60% of the seeds from the productive zone of a white spruce cone. However, because they did not provide information on the size of the cones or the number of filled seeds per cone, these results cannot be compared. The seed-destroying capacity of S. neanthracina on black spruce cones could not be determined in this study because no cones were infested. But, Prévost et al. 1988, reported that ca. 50% of the seeds of a black spruce cone could be destroyed.

Table 3. Impact of Lepidoptera on volume and number of filled seeds of black and white spruce cones, Ontario, 1988.

		Healthy cones		Infested cones			
		N	$\bar{x}\pm SE$	$\bar{x}\pm SE$	T	P	DF
Cone volume	Sb	19	2.79±0.12	2.74±0.24	0.2	0.85	27
	Sw	15	3.90±0.27	3.37±0.21	1.6	0.13	26
No. filled seeds/cone	Sb	19	37.1±4.2	34.6±3.2	0.5	0.64	33
	Sw	15	59.4±4.7	51.7±5.7	1.0	0.31	27

Table 4. Impact of the spruce cone maggot on volume and number of filled seeds of white spruce cones, Ontario, 1988.

	Healthy cones		Infested cones			
	N	$\bar{x}\pm SE$	$\bar{x}\pm SE$	T	P	DF
Cone volume	26	4.00±0.25	2.96±0.17	3.5	0.0012	43
No. filled seeds/cone	26	61.5±3.81	17.65±1.68	10.6	0.0000	34

Among the 5 orchards studied, a total of only 12 seeds were infested by a Cecidomyiid larva. Consequently no statistical analysis was performed. The identity of this Cecidomyiid is currently unknown. However, I suspect that it is the same species that Tripp (1955) discovered in white spruce seeds and referred to as Species A. Seeds infested by this species exibited no apparent external evidence of attack such as occurs with the spruce seed gall midge, Mayetiola carpophaga (Tripp), attack, an observation also made by Tripp (1955). Adults emerging from these infested seeds were sent for identification.

These preliminary results revealed no clonal differences in the proportion of cones damaged by S. neanthracina, and by Lepidoptera spp. when cone abundance is high. Additional studies with different levels of cone and insect abundance are needed to determine if clones of black and white spruce vary in susceptibility to insects infesting cones and seeds (Roques 1986).

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ENVIRONMENTAL ARCHITECTURE - PREVENTING LOSS OF SEED PRODUCTION TO INSECTS IN BLACK AND WHITE SPRUCE SEED ORCHARDS

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ABSTRACT

Environmental architecture stresses modification of seed orchard surroundings to minimize the immigration of cone and seed insects. It is suggested as a control strategy for spruce budworm, Choristoneura fumiferana (Clem.), and spruce cone maggot, Strobilomyia neanthracina Michelsen, two damaging species of spruce cones. A first approach is to establish orchards away from forests whose tree composition contains abundant spruce and balsam fir. Where this is not possible the surrounding forests must be groomed to promote healthy trees, and spruce and balsam fir should be removed to prevent budworm and cone maggot from developing near the orchard. Pollen dilution zones, 500 m clearcuts, should be established around orchards to create a barrier for migrating insects. To increase the effectiveness of the zone, two rows of deciduous windbreaks should be planted. The windbreaks serve to mask the orchard visually and by olfaction from insects originating in the forest. Also, it would physically filter insects being blown into the orchard and interfere with local insect dispersal by generating turbulent air. Moreover, the windbreaks may be compatible with pollen management.

RÉSUMÉ

La géoarchitecture met l'accent sur la modification des environs du verger pour réduire la migration des ravageurs des cônes et des graines. C'est proposée comme stratégie de lutte contre la tordeuse des bourgeons de l'épinette [Choristoneura fumiferana (Clem.)], et la mouche granivore de l'épinette (Strobilomyia neanthracina Michelsen), deux ravageurs des cônes de l'épinette. Idéalement, il s'agirait d'établir les vergers à l'écart des forêts qui contiennent des peuplements d'épinettes et de sapins baumiers. Ceci n'étant pas toujours réalisable, les forêts environnantes devraient être nettoyées afin d'améliorer la santé générale des arbres, et épinettes et sapins baumiers devraient en être éliminés afin d'empêcher la tordeuse des bourgeons et la mouche granivore de se reproduire à proximité du verger. Des bandes d'isolement de sources de pollen indésirables (coupes à blanc de 500 m), devraient entourer les vergers. En soi, ces zones feront obstacle à la migration des ravageurs, mais on peut les rendre plus efficaces en y plantant deux rangées de feuillus brise-vent. Ces brise-vent dissimuleront le verger à la vue et à l'odorat des insectes provenant de la forêt. De plus, ils filtreront littéralement les insectes transportés par le vent vers le verger et empêcheront la dispersion des insectes locaux en créant une zone de turbulence. Qui plus est, ces brise-vent pourraient contribuer à la gestion des pollens.

INTRODUCTION

Necessity to regenerate our harvested forest lands has prompted the recent proliferation of seed orchards in eastern Canada. Seed orchards represent large investments for security of our place in future newsprint and lumber markets, and need to be protected against depredation by insects.

Environmental architecture alters flora and is a silvicultural method of insect control. Other terms used in reference to forest structure and the influence it may have on insect populations are vegetation structure (Perry and Maghembe 1989) and forest landscape (Schowalter 1988). Environmental architecture and silvicultural control suggest an intentional manipulation of flora to keep insect populations in check, whereas vegetation structure and forest landscape simply describe the associations of flora in which insects are found. Environmental architecture and silvicultural control may in turn be differentiated, in that the latter is the alteration of the flora to decrease forest susceptibility which minimizes insect damage to forest products. These alterations may involve thinning, pruning, presalvage and salvage cuts as well as planting trees on the right sites. Environmental architecture also decreases forest susceptibility through thinnings and cuts, and correct planting, but goes somewhat further. It involves the intentional modification of insect behavior and insects' physical movement through vegetation alteration. Silvicultural control simply relates stand susceptibility to insect density and damage and attempts to minimize its susceptibility without any knowledge of the relationship between trees and insects at an organismal level. Thus, environmental architecture is process-oriented, whereas silvicultural control uses the "black box" approach.

Although the term environmental architecture is new, the concept is not. There is a basis to believe that forest structure will influence herbivore populations, in that monocultures frequently suffer greater feeding damage by insects than do polycultures (Gibson and Jones 1977). Cromartie (1981), Stanton (1983) and Kareiva (1983) strongly suggest that plant community structure affects host plant finding by insects. Prokopy and Owens (1978; 1983) and Visser (1986) indicate that visual and olfactory interferences of other plants in mixed stands diminish the ability of insects to locate host plants.

I have taken a theoretical approach to demonstrate how environmental architecture may be applied to regulating populations of cone and seed insects in spruce seed orchards. There is no guarantee that cone and seed insects will behave as theory dictates, but it is time to investigate how forest structure influences insect behavior and apply these findings to the prevention of insect damage of our cone crops.

Plant Community Structure and Insect Herbivore Populations

Monoculture versus polyculture as a growing strategy has been hotly debated, because of the implications for pest management in agro- and forest ecosystems (Watt 1965; van Emden and Williams 1974; Risch et al. 1983; Redfearn and Pimm 1987). Many insect outbreaks have occurred in monocultures in both agroecosystems (van Emden and Williams 1974) and forest ecosystems (Gibson and Jones 1977). Elton (1958), MacArthur (1955), Margelef (1968) and Odum (1971) have attributed such outbreaks to the simple ecosystem structure of monocultures.

In forest ecosystems, insect densities often increase to such proportions that they become pests in monocultures. Innocuous insects have developed as important pests, especially in plantations of the sub-tropical and tropical regions (e.g., Gray 1972; Gibson and Jones 1977; Perry and Maghembe 1989). In North America, white pine weevil, Pissodes strobi Peck, becomes excessively abundant in pure stands of white pine, Pinus strobus L., but when pine is grown in mixed stands infestations are low (Graham 1926; MacAloney 1930). Furthermore, as herbivore insect biomass increases, the number of insect species decreases when comparing insects in old-growth Douglas-fir, Pseudotsuga menziesii (Mirb.) Franco, forests to regenerating monocultures in western United States (Showalter 1988). Plant diversity appears to play an important role in maintaining the balance of nature and strongly affects herbivore insect population dynamics (Pimentel 1961; van Emden and Williams 1974). Stanton (1983) demonstrated that plant diversity was negatively related to herbivore loads, whereas host plant density was positively related.

Although monocultures are generally more susceptible to insect attack, some plants grow well naturally as monocultures. For example, black spruce, Picea mariana (Mill.) B.S.P. (Vincent 1965; Johnston 1977), red pine, Pinus resinosa Ait. (Benzie 1977a), and jack pine, P. banksiana Lamb. (Benzie 1977b), grow in pure stands and are not normally devastated by insects. When considering forest monocultures, a distinction must be made between those species naturally growing in pure stands and those species growing in mixed stands. It is possible that mixed-forest species such as white spruce, Picea glauca (Moench) Voss., when grown in plantations would suffer greater damage by spruce budworm, Choristoneura fumiferana (Clem.), than would black spruce, because white spruce is normally associated with other tree species (Nienstaedt 1957; Fowells 1965).

Forest Structure and Host Plant Selection by Herbivores

Forest structure reflects the spatial configuration of host plants which in turn determines the probability of host plant selection by the herbivore. To understand how herbivorous insects may be prevented from damaging crops by environmental architecture, we must first understand how insects locate and select host plants. It is generally agreed that insects select host

plants through a series of decisions which are: 1) host plant habitat finding, 2) host finding, and 3) host acceptance (Kogan 1981; Vinson 1976, 1981, 1984; Klingauf 1987). Environmental architecture has the intention of disrupting the host plant selection process at steps one and two. These steps are important to spruce seed orchard managers because an interference with finding habitats and host also can prevent the movement of cone and seed insects from the surrounding forests into the orchard. If more was known on the host selection process of these insects, disruptive stimuli induced by vegetation manipulation could be used to prevent the immigration of insect pests.

Even though herbivorous insects are a constant threat to our crops, we only have a general notion of how some insects find those crops. For most insects, our knowledge of the host plant-finding behavior is poorly developed to nonexistent. It is the adult female which actively selects the host plant habitat for the larvae, however, ballooning larvae can redisperse themselves passively on wind currents to other habitats. Recent reviews by Prokopy and Owens (1983), Stanton (1983) and Visser (1986) indicate that insects use sight and olfaction to locate host plants for feeding, mating and oviposition. Sight and olfaction may each act at close and far range depending on the insect species and may stimulate the insect in a given sequence to find its preferred host plant (Prokopy and Owens 1983).

I will limit the discussion of host habitat and host plant finding by cone and seed insects to the spruce budworm and to cyclorrhaphous flies, the group to which the spruce cone maggot, Strobilomyia neanthracina Michelsen (Anthomyiidae), belongs. The spruce budworm is an important pest feeding on cones of black spruce (Schooley 1980; Kondo and Taylor 1985; Prévost et al. 1988) and white spruce (Kondo and Taylor 1985). The spruce cone maggot, a transcontinental species, also has severely damaged spruce cone crops (Kondo and Moody 1987; Moody 1988).

Spruce Budworm

Host habitat and host plant finding

For the spruce budworm, host habitat and host plant finding is not a major problem, as this specialist herbivore inhabits the boreal forest where food is readily available (Watt 1965). The spruce budworm feeds on both cones and foliage of white and black spruce, as well as on a few other coniferous species, and thus is not strictly a cone and seed insect. However, when on black spruce it appears to prefer cones (Prévost and Laing 1986), but feeds readily on both cones and foliage of white spruce (pers. observ.).

Unlike obligate cone and seed insects, the spruce budworm does not disperse in search of other sources of cones during years when cone production is poor and survives by consuming spruce foliage (Lavallée and Hardy 1988). The causes of spruce budworm

moth dispersal have not yet been conclusively identified, but the concentrations of female sex pheromone may induce dispersal (Sanders 1987). Local and long-range dispersal of spruce budworm is achieved both by females and males (Greenbank et al. 1980). Local dispersal also occurs by ballooning first and second-instar caterpillars (Régnière and Fletcher 1983). When spruce budworm adults disperse, it must recognize host habitat in order to alight on host trees. Adults probably utilize vision and olfaction ultimately to find a suitable host tree for oviposition, whereas ballooning larvae are most likely guided by wind although olfaction may be a factor in locating a host tree on which it can feed.

a) Vision

Dispersing spruce budworm moths probably locate potential host plants using a visual cue and drop almost vertically when they do so (Greenbank et al. 1980). The spires of dominant trees which emerge through the forest canopy are thought to be a visual cue that is indicative of host plants and terminates flight (Mattson et al 1988). Other Lepidoptera have also been observed using plants extending above the surrounding vegetation as a cue for finding host plants for oviposition (Wiklund 1984).

b) Olfaction

Dethier stated "no one attractant alone performs the service of guiding an organism to its proper habitat, or mate, or food", however chemical attractants offer precise guidance (Wright 1958). Not much is known of the importance of host plant odors in attracting spruce budworm adults to host habitat and host plants. This is the case for many moth species of economic importance (Ramaswamy 1988). Nevertheless, it is well known that adults do respond to odors for mating purposes (Sanders 1987), and for oviposition (Staedler 1974) and therefore, probably respond to volatiles emitted from host plants. D-alpha and L-beta pinene stimulate oviposition in spruce budworm and perhaps draw gravid females from a distance to spruce trees, the preferred hosts for oviposition (Wilson 1963; Renwick and Radke 1982).

Little is known on how host odors affect ballooning first-instar and second-instar. Second-instar spruce budworm can discriminate between odors of different host plants (Ascoli and Albert 1985) and during dispersal, a second instar may orient itself towards spruce trees by lengthening or shortening the silk thread (Ascoli 1985) as occurs in the Douglas-fir tussock moth, Orgyia pseudotsugata (McDunnough) (Mitchell 1979). In spite of this potential ability for orientation, it is probably not very efficient as ballooning larvae are largely at the mercy of the wind.

Cyclorrhaphous Flies

Host habitat and host plant finding

For the spruce cone maggot, finding spruce habitat and spruce trees may not normally be a problem because it overwinters in the humus layers at the base of spruce. However, it must find the proper host plant tissue at the suitable stage of development for oviposition. Adult emergence from the overwintering site is synchronized with pollination when the adult flies up to alight on the spruce branches (Tripp 1954; Ruth et al. 1982). Eggs are laid on the spruce flowers and the larvae feed on cone tissue and seeds. When cones are produced from year to year at the same site, it is expected a closed cycle is established between the spruce cone maggot populations and the spruce. However, during years when spruce cone production is poor, the spruce cone maggot adult is obliged to migrate into areas where spruce cone production is more bountiful. In this situation, finding spruce habitat and host trees are important problems for the spruce cone maggot. The fly probably depends on both visual and olfactory cues to find cones on which to lay eggs.

a) Vision

Host habitat finding could be classified as long-range detection. A spruce cone maggot adult leaving the surrounding forest and entering a seed orchard, would detect the horizon line between the surrounding forest canopy and the sky. As it approaches the orchard trees, the distance to them would be reflected as their contrast with the background and their size (Prokopy and Owens 1983). From a distance the fly could probably detect color in the foliage, although details would be lacking (Prokopy and Owens 1983). The spruce cone maggot is oligophagous and Prokopy and Owens (1978) suggested that such feeding specialists are also visual specialists. The preferred spectral zone of the larch cone fly, Strobilomyia melania (Ackl.)(Anthomyiidae), was demonstrated by adult attractance to sticky traps whose wavelengths reflected maximally about 542 nm (Roques 1984). Another anthomyiid fly, the onion maggot, Delia antiqua (Meigen), was attracted to sticky traps which reflected maximally between 400 and 470 nm (Vernon 1986). The spruce cone maggot could also be attracted by a preferred spectral zone and thus find its host habitat.

As the spruce cone maggot approaches trees in the preferred spectral zone, it would recognize individual tree shapes and alightment on the host could be encouraged by the quality of light reflected from the foliage. This stimulus is important for aphids alighting on host plants (Kennedy et al. 1961). On the spruce branch, the spruce cone maggot adult seeks female flowers as oviposition sites, how it is unknown. The searching behavior of the larch cone fly (Roques 1984; 1986; 1987) could be extrapolated to the spruce cone maggot. The larch cone fly eye is most sensitive to wavelengths reflected by the host tree foliage and

least sensitive to wavelengths reflected by the flowers (Roques 1984). Thus, the larch cone fly could detect flowers as dark ellipsoids against a green foliage, once in the tree crown. Tephritid flies discriminate between shapes placed in trees (Shervis et al. 1970; Prokopy, 1977; Prokopy and Owens 1978).

b) Olfaction

A spruce cone maggot adult leaving the surrounding forest and entering a spruce seed orchard would perceive chemicals emitted from spruce foliage and thus could orient itself to its new host plant habitat. Although no work exists to show that the spruce cone maggot adult responds to host plant odors, it has been demonstrated that other anthomyiid species do (Matsumoto and Thorsteinson 1968; Prokopy et al. 1973; Finch and Skinner 1974; Hawkes 1974; Guerin et al. 1983).

The spruce cone maggot, being a specialist herbivore, would be very sensitive to volatiles emitted by spruce trees. The odors perceived could either be specific to spruce trees or be a particular blend of constituent chemicals which would identify these as spruce trees (Visser 1986). Finding the host habitat and host plant also could be guided by odor-conditioned anemotaxis as it is in many insects (Kennedy 1983; Visser 1986). Ultimately, the spruce cone maggot adult upon alighting on the spruce branches, could detect female flowers by visual contrast with the foliage and/or by chemicals emitted from the female flowers. Roques (1987) demonstrated that the reproductively-mature larch cone fly was most sensitive to odors emitted by larch flowers in the phenological state selected for oviposition (Roques 1987).

As Kennedy (1983) underlined, it is a formidable task for a flying insect to determine an odor source in the field, which represents food, a mate or an oviposition site. Spruce cone maggot adults following odor plumes must contend with the rupture of plumes induced by wind gusts and air turbulence. To enhance their ability to find host plant habitats and ultimately host plants, spruce cone maggot adults probably use vision in concert with olfaction.

Management of Seed Orchards and Environmental Architecture

The very nature of spruce seed orchards demands that they are monocultures. Seed orchards consists of genetically-superior trees where maximum exchange of genetic material between them is encouraged by planting these trees in close proximity to each other. However, this arrangement will enhance the ability of spruce budworm and spruce cone maggot to discover its preferred host plants and consequently present a management problem for seed orchardists. To minimize the probability of discovery by insects, spruce orchards should not be much larger than 8 ha, the minimum size recommended by the Ontario Ministry of Natural Resources (1989).

Black spruce normally grows in monoculture and its foliage suffers little spruce budworm damage (Blais 1957; Prévost and Laing 1986). However, black spruce cones are susceptible to damage, because they are available to spruce budworm as they emerge from their overwintering sites (Prévost and Laing 1986). White spruce cones also are available to spruce budworm as they flush a few days before those of black spruce (pers. obser.). Thus, cones from both spruces in seed orchards are equally susceptible to spruce budworm, even though both tree species grow normally in pure or mixed stands.

The most direct method to avoid insect infestations, especially by spruce budworm, is to establish spruce seed orchards away from forests which contain a large component of spruce and balsam fir. There is an example of this in northwestern Ontario at the O'Connor seed orchard. It is a black and white spruce seed orchard planted in an abandoned agriculture field where the surrounding forests are deciduous. Although the migratory habit of the spruce budworm always poses a threat to seed orchards, their arrival in an orchard can be signaled using pheromone traps (Sanders 1988). Isolating spruce seed orchards will reduce insecticide applications and avoid contaminating pollen entering the seed orchard from the surrounding forests.

Spruce seed orchards cannot always be isolated from forests harboring spruce budworm or other coniferophagous insects. In this scenario, pest management should not be limited only to the orchard. The adjacent forests should be made less susceptible to spruce budworm to prevent dispersal of larvae and adults into the orchard. Silvicultural approaches that can be taken are: 1) encourage a vigorous forest by thinning, 2) do not allow balsam fir to develop, and 3) increase the nonhost component of the forest. Even though these concepts are not new, they are frequently ignored. For example in northwestern Ontario, spruce nursery stock (Bray 1985), plantation seedlings and seed orchard seedlings (pers. observ.) planted next to forests harboring spruce budworm have been infested with second-instar larvae and subsequently treated with insecticides to minimize damage.

Damage in spruce seed orchards could be further limited by modifiying a practice already in place in many orchards. Pollen dilution zones, 500 m clearcuts, are recommended to isolate the orchard from the adjacent forests to minimize contamination by foreign pollen (Simpson and Smith 1988; Ontario Ministry Natural Resources 1989). This practice in itself acts as a barrier to cone and seed insects flying or ballooning in from the forest to the orchard; dispersing insects in the zone would have to contend with winds. A modification, which has the potential of further preventing insect dispersal into the orchard, is the establishment of two rows of windbreaks in the pollen dilution zone. Windbreaks could consist of deciduous tree species with a dense crown such as Lombardy poplar, Populus nigra L. var. italica Muenchh., and white ash, Fraxinus americana L., planted 200 and 400 m from the orchard's edge. Red pine also has been suggested (Simpson and

Smith 1988). Ideally, establishment of windbreaks should be carried out a few years before the seed orchard is established.

Use of windbreaks as a pest insect management tool has not been extensive probably because of the time required to establish them. Windbreaks would serve in one capacity as a mask for the orchard, in another capacity as a filter, and lastly as a generator of turbulent air. Studies of the interaction between windbreaks and insect dispersal have focused on the creation of turbulent air (Pasek 1988).

The windbreak would act both as a visual and olfactory mask for the orchard. Locally-dispersing adult spruce budworm and spruce cone maggot leaving the forest first would visually contact the outer row of non-host windbreak trees. Although, the spectral reflectance of Lombardy poplar and white ash relative to black and white spruces is not known, they are different, and probably would not be attractive to either insect species. Furthermore, the first volatiles encountered would be those of the deciduous tree species and would further discourage either insect species from searching the general direction of the orchard. If either insect species got beyond the first windbreak, they would encounter the second windbreak and would continue to search randomly for a suitable host tree. Conifers related to spruce such as red pine may have visual and olfactory qualities attractive to spruce cone and seed insects and thus may not be suitable for windbreaks.

The delay in finding a host tree may be important for the spruce cone maggot, because oviposition occurs during a tight biological window when conifer flowers are open for pollination. It is unknown how long after pollination oviposition can occur for cones to be infested. Long-range dispersal of the spruce budworm has been studied, but not much is known about its local dispersal. We need to know the efficiency of the spruce budworm in finding host plants and the distances it travelled in local searches to determine the effectiveness of windbreaks on local dispersal. Ballooning spruce budworm larvae from the surrounding forests would encounter olfactory disruptive stimuli of the windbreaks before encountering the seed orchard. How much control these larvae have in alighting on a suitable host plant and directing their dispersal is not known but windbreak trees would provide visual and olfactory disruptive stimuli thus masking the orchard.

Windbreaks also can act as filters for insect stages which can fly, such as spruce budworm adults, and also for stages that are passively blown by the wind such as spruce budworm larvae. During relatively windy days, a windbreak could intercept blown insects and physically remove them from the air. Apart from interfering with insect dispersal, windbreaks would certainly help prevent foreign pollen from entering the orchard.

Finally, windbreaks would increase air turbulence in the pollen dilution zone and hence, influence insect dispersal (Pasek 1988). A windbreak interrupts the free flow of air and creates

downdrafts and sheltered zones on the leeward side (Lewis and Stephenson 1966; Lewis and Dibley 1970). The degree of sheltering and downdrafts varied with the permeability of the windbreak, the less permeable barriers provide the greatest shelter and more downdraft. Insects accumulate leewardly due to wind flow and not to visual cues (Lewis and Dibley 1970) or physical size (Lewis and Stephenson 1966). Lewis and Stephenson (1966) found that at 0 and 25% permeability most flying insects gathered within three heights of the windbreak, whereas more permeable barriers allowed insects to gather much further leeward. Insects tend to be found where wind speed is slow enough to allow them control of their flight.

Windbreaks surrounding a seed orchard should be as impermeable as possible, to concentrate insects close to the windbreak. When calculating impermeability of windbreaks consideration must be given to the spacing of trees, crown density, and time of leaf flushing especially if deciduous species are planted. For the windbreak to act as a mask against invasions by the spruce cone maggot, it may be important to plant a deciduous species which flushes earlier than or at the same time as spruce pollination. It would also be important to prevent ballooning larvae from invading the seed orchard; they would be greatly influenced by windbreak-generated downdrafts whose strength is dependent on the degree of impermeability. Foreign pollen would be influenced in the same way and could be expected to fall on the ground.

Yellow herbaceous flowers are attractive to larch cone flies as an energy source to maintain flight activity and as nourishment for egg maturation (Roques 1984, 1986). This requirement is important for the larch fly if egg-laying is to occur. If the same is true for the spruce cone maggot, an important preventative measure to discourage spruce cone maggot adults may be to keep the orchard mowed when the fly is maturing sexually and is ovipositing.

SUMMARY AND CONCLUSIONS

Environmental architecture exploits the fact that herbivorous insects respond to and are influenced by differences in plant texture. Two windbreaks in the pollen dilution zone are suggested as a barrier between the surrounding forest and a spruce seed orchard. Such a barrier will help prevent insect damage when the forest has a heavy component of spruce and balsam fir. The spruce cone maggot and spruce budworm, specialist herbivores of spruce, probably are attracted to spruce visually and by olfaction. A windbreak consisting of deciduous trees would mask the orchard from the insects because it would be visually and chemically different from the orchard trees. Windbreaks would also act as a physical filter for insects blown across the pollen dilution zone into orchard. Finally, plant texture also interferes with the free flow of air and hence creates turbulences which could interfere with local dispersal of spruce budworm and spruce cone maggot.

The strategy proposed here is a new solution to a relatively new problem in Canadian forestry. The strategy is based on exploiting the behavior of spruce budworm and spruce cone maggot, about which we know very little. Inferences can be made from what is known about closely related species to initiate general studies of this strategy. Eventually more exacting studies must be conducted to discover the intimate relationships that these specialist insects have with their host plants, but this strategy should be implemented on at least a limited basis.

Use of windbreaks as a pest management tool has not been extensive, probably because we have little knowledge of how insects find host plants and because it takes time to establish windbreaks. Windbreaks promise to be a viable, long-term approach in minimizing insect damage to seed orchards reducing the need for insecticides.

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RED SQUIRRELS AND CONE CROPS: DAMAGE AND MANAGEMENT

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ABSTRACT

Squirrels are the major vertebrate pest of cone crops and can substantially reduce the availability of cones by harvest. Cone depredation by the red squirrel, Tamiasciurus hudsonicus (Erxleben), on pine and spruce is reviewed. The following management strategies are discussed: utilization of cone caches; early harvesting; repellents; mechanical barriers; squirrel relocation; shooting, poisoning and kill-traps; and cultural practices. Use of cone caches and early cone-harvesting are recommended; repellents and live-trapping are considered as potentially suitable control options. Permanent removal by lethal methods is suggested as a last resort.

RÉSUMÉ

Les écureuils sont les principaux vertébrés ravageurs des cônes et peuvent grandement réduire l'importance de la récolte. On examine ici les déprédations causées par l'écureuil roux, Tamiasciurus hudsonicus (Erxleben), dans les forêts de pins et d'épinettes. On présente ensuite les stratégies de répression suivantes: utilisation de caches de cônes, récolte hâtive, emploi de répulsifs, barrières mécaniques, relocalisation des écureuis, élimination au moyen d'armes à feu, de poisons et de pièges, ainsi que le recours à certaines méthodes culturales. On recommande l'emploi de caches de cônes et la récolte hâtive; de plus, les répulsifs et les pièges permettant de capturer l'animal vivant constituent des choix également acceptables. L'élimination permanente au moyen de mesures entraînant la mort des animaux n'est suggérée qu'en dernier ressort.

INTRODUCTION

The red squirrel, Tamiasciurus hudsonicus (Erxleben), is a common inhabitant of boreal forests of North America where it is the primary vertebrate predator of cones of all conifer species (Halvorson 1986). Red squirrels feed on a variety of foods (Klugh 1927, M.C. Smith 1968), but populations fluctuate with the size of conifer cone crops (Kemp and Keith 1970, Flyger and Gates 1982). Conifer seeds may provide half of the annual energy requirements of the red squirrel (Finley 1969) and buds also are eaten during winter and early spring (Rusch and Reeder 1978). One or two litters of three to four offspring are produced per year (Millar 1970, Kemp and Keith 1970) depending on food resources available. Life expectancy can exceed eight years, but 90% of individuals in wild populations live less than three years (Davis and Sealander 1971).

Red squirrels threaten to reduce cone yields in managed stands (Cecich and Rudolph 1982, Hurly et al. 1987) and some authors (e.g., Smith and Aldous 1947, Finley 1969) believe that they retard natural regeneration. Squirrels also affect the growth of conifers by debarking and girdling (Sullivan and Sullivan 1982, Sullivan and Moses 1986, Brockley and Elmes 1987, Sullivan and Vyse 1987), and through bud and shoot removal (Viidik 1973, Prevost et al. 1988).

Seed orchards are needed to supply increasing demands for the high quality genetically superior seed used in regeneration programs. It is unlikely that the widely spaced trees and trimmed vegetation found in seed orchards provide suitable cover and nesting requirements for red squirrels to maintain territories. However, management may be required when squirrels move into orchards to collect cones as a winter food supply. We review the impact of red squirrels on pine and spruce production and describe several management techniques for reducing damage in seed orchards and cone collection areas.

CONE DEPREDATIONS

Pine

Seed maturity generally coincides with an onset of cone removals by the red squirrel in jack pine, Pinus banksiana Lamb., (Cecich and Rudolph 1982) and other conifers (Klugh 1927, Finley 1969). Significant cone depredations have been recorded for jack pine (30% - Rauf et al. 1985, de Groot 1986); white pine, P. strobus L. (100% - Pulling 1924); ponderosa pine, P. ponderosa Laws. (60 to 80% - Squillace 1953, 66% - Schmidt and Shearer 1971, 17 to 100% - Halvorson 1986); sugar pine, P. lambertiana Dougl. (54% - Tevis 1953); and limber pine, P. flexilis James, and southwestern pine, P. strobiformis Englem. (75-83% - Benkman et al. 1984). Red squirrels also collect cones of lodgepole pine, P. contorta Dougl. (Cox 1911, Finley 1969, Elliot 1974).

Spruce

Populations of red squirrels are higher in spruce than in pine stands (Kemp and Keith 1970, Rusch and Reeder 1978). Cones of white spruce, Picea glauca (Moench) Voss, appear to be favoured over those of black spruce, P. mariana (Mill.) B.S.P. (Brink and Dean 1966, M.C. Smith 1968, Prevost et al. 1988). Extensive depredations have been observed on both species especially when cone crops are small (Fogal and Lopushanski 1984, West 1989). Cones of Englemann spruce, P. englemannii Parry, and blue spruce, P. pungens Engelm., are also collected in high numbers (Finley 1969).

MANAGEMENT TECHNIQUES

Use of cone caches

Perhaps the simplest management strategy to control squirrels in a seed orchard is to regard them as beneficial animals rather than pests. Hurly et al. (1987) concluded that harvesting cones from squirrel caches is a practical approach which avoids the expense of collecting the cones by hand. Cones should be collected during the first month following the peak caching period to maximize seed viability. To be of value, caches must be easily found and contain a large proportion of viable seeds.

The benefits of cache use must be weighed against the damage caused by squirrels. Removal of cones by squirrels from the branches can lead to stem breakage and the resulting wounds may become fungal infection sites. Bud damage may increase when squirrels turn to an alternative food supply after caches are raided and cones harvested by cone collectors. The potential significance of bud feeding was illustrated by Rusch and Reeder (1978) who reported that one squirrel consumed an average of 639 jack pine buds and 35 cones in one day. As a final consideration, a proportion of the cones will be consumed and not cached; this loss may be significant where the cone supply is close to demand.

Early cone harvesting

Early harvesting of cones (last 2 weeks of August), before squirrels begin intensive harvesting, has met with some success for Scots pine, P. sylvestris L., red pine, P. resinosa Ait., and white spruce, provided that seed is subsequently ripened under controlled conditions (Hurly et al. 1987 and references therein). For species that bear serotinous cones, such as jack pine (Rauf et al. 1985) and black spruce (West 1989), cones can be collected after they ripen but before the period of intensive harvesting by squirrels. Early harvesting could result in a threefold increase in available cones of jack pine (Rauf et al. 1985) and records of seasonal caching of white spruce cones (Wagg 1964) indicate that harvesting between 22 and 30 August could double yields made after 15 September. As many as 17 times the black spruce cones

available in October could be obtained by late August collections (West 1989).

Collecting cones before squirrels begin their major harvest will probably lead to reduced yields of viable seed (Cecich and Rudolf 1982), particularly from non-serotinous cones (Hurly et al. 1987). To effectively use this technique, maturity dates for various cone crops in major collection areas need to be determined (e.g. Curran et al. 1987). The gain in cone numbers resulting from early collections must be balanced against an estimated loss in seed viability.

Repellents

Repellents incorporating predator odors have been suggested by Sullivan (1987) as a direct damage control technique for red squirrels. Preparations of predator odors have suppressed feeding in other herbivores such as snowshoe hares (Sullivan et al. 1985a), black-tailed deer (Sullivan et al. 1985b), voles (Sullivan et al. 1988a); and repelled pocket gophers (Sullivan et al. 1988b). Mammalian predators of the red squirrel include the lynx, coyote, and weasel (Rusch and Reeder 1978); red fox (Johnson 1970), and marten (Klugh 1927). Extracted compounds from glands and wastes of these animals, or synthesized isolates could be used to begin the search for a useful squirrel repellent. Synthetic weasel odour and sunflower seed, an alternative food; and marten scent may soon be tested for their effects in reducing squirrel damage (pers. comm., T.P. Sullivan, Applied Mammal Research Institute, B.C.; Y. Prevost, Lakehead University, Ont.).

Chemical repellents such as naphthalene and paradichlorbenzene crystals may be useful in small areas such as outdoor cone storage sheds. Other repellents suggested for squirrels include Biomet 12, R 55 repellent and Thiram (Fitzwater 1983).

Mechanical barriers

Mechanical barriers have been used with some success to prevent cone removal by red squirrels. Tackle (1957) prevented cone depredations by banding ponderosa pine with smooth aluminum sheets 45 cm in width, while 15 cm and 30 cm wide bands proved to be ineffective. He suggested that cheaper materials, such as plastic, might be used. Krugman and Echols (1963) provide a design for an 45 cm aluminum band that allows for several years expansion from radial stem growth. Bands should be smooth to prevent squirrels from climbing and installed 2 m from the ground. Bands are useless if the branches can be reached from the ground or nearby trees. Tackle (1957) indicated that a minimum distance of 2.1 m between trees is necessary to discourage squirrels from jumping from one tree to another. Costs of installation and material would likely prohibit the use of bands in large areas.

Jackson (1986) indicated that mesh fences about 1.2 m high and topped with an electrified wire 5 cm above the mesh would keep

squirrels out of nursery areas. However, the cost of fencing is likely too expensive for seed orchards.

Squirrel relocation

Squirrels can be easily caught in live-traps and relocated to an area from which their return would be unlikely (e.g., across a river). Live-traps should be baited and left open to attract the animal and then rebaited and set (Marsh and Howard 1977). Peanut butter is a commonly used bait, although other foods such as raisins and sunflower seeds are effective. Traps should be checked at least daily to remove squirrels and other trapped animals. When natural foods are abundant, trapping success may be reduced. Trapping is probably best restricted to the period when cones are about to ripen and become attractive to squirrels.

Re-invasion of squirrels to the vacated area from another territory can be a problem, particularly in natural stands. Repopulation is immediate and continuous following removal of any small mammal population from a given area (Sullivan and Sullivan 1982). It may be necessary to trap in areas surrounding the seed orchard to reduce the rate of reinvasion. The number of traps needed to protect crop tree areas would have to be determined for each seed orchard and will depend on the size of the squirrel population and the size of the orchard.

Shooting, poisoning and lethal traps

The red squirrel is an important furbearer in Canada (Kemp and Keith 1970) and a popular food item in some areas. Cooperation between seed orchard managers and local hunters and trappers could be mutually beneficial.

Poison baits (e.g., Matschke et al. 1982) can be effective but the harmful effects on non-target animals would restrict or prevent their use. Zinc phosphide is the common toxicant used for squirrels. Anticoagulants in cereal baits may also be effective for control but if the squirrels store the baits, the use of anticoagulants should be discontinued (Marsh and Howard 1977). Anticoagulants may take up to 4 weeks to cause death.

Lethal traps such as ordinary wood snap-traps used for rats could be used in small, contained areas. Baits should be fastened to the trigger with string, otherwise some squirrels may steal the baits without being caught (Marsh and Howard 1977). Because lethal traps may also catch birds or other animals, they should be used with the advice of a wildlife or pest control officer. Like live-traps, snap traps should be baited without setting for several days before being used (Marsh and Howard 1977).

Cultural practices

Complete removal of cones, as should be done annually to rid seed orchards of overwintering insect pests, would eliminate a

fall and winter food source and discourage squirrels from remaining in a managed area. Squirrels are further discouraged by the control of underbrush, which provides alternative food sources and cover from predators.

Thinning reduces red squirrel densities and increasing the area of thinning to more than 100 ha may reduce damage by reducing immigration from surrounding forests (Sullivan and Moses 1986). The creation of inhospitable buffer zones surrounding cone collection areas would further discourage immigration.

RECOMMENDATIONS

The techniques used for the management of red squirrels depend primarily on the severity of damage and management objectives of the seed orchard or cone collection area. Other important factors to consider are cost, available resources, and wildlife regulations.

We recommend that consideration be given initially to techniques that allow for the continued presence of squirrels. These techniques include making the use of squirrel caches, early and complete cone-harvesting or a combination of both. Repellents could be considered next, but additional research is needed to determine the efficacy of this technique. If squirrels cause unacceptable damage in a seed orchard not subject to an immediate influx of squirrels from surrounding areas, we recommend that squirrels be live-trapped and relocated. Shooting is the only lethal method recommended to remove squirrels but this is a last resort and should be done in consulation with wildlife and pest control authorities.

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